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FIFTY YEARS OF THE AMERICAN SOCIETY OF NATURALISTS

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IN this jubilee year of the American Society of Naturalists it is a source of gratification to the present members to know that seven of the original 109 members are still with us in body, mind and scientific activity. I call the roll of this honored company, and in the name of the society extend to each of them our congratulations and best wishes: Henry H. Donaldson, Simon H. Gage, Samuel Henshaw, C. Hart Merriam, Henry F. Osborn, William B. Scott, Edmund B. Wilson.

Some of these founders who have seen the whole history of this society should have been chosen to give the historical address on this occasion. Unfortunately, the society meets but once a year and a vote at one meeting can not be rescinded until the next annual meeting, and as I was not present to make my protest at the meeting last year, the honor and duty of giving this address were assigned to me. No doubt the younger members who did this thought I was old enough to have been a founder of this society or even to have answered "Present" to the question once propounded to Job, "Where wast thou when I laid the foundations of the earth?", but I protest that I have been a member of the Society for only thirty-eight years.

On at least three occasions in the past some of the founders of the society have spoken informally of its early history. In 1901 Professor C. S. Minot did this at the Chicago meeting of that year (see *Science*, Vol. 15, No. 372). At the Philadelphia meeting in 1914 Professor S. F. Clarke spoke briefly of the founding of the society,

and at the Chicago meeting of 1920 Professors J. S. Kingsley and W. N. Rice filled the gap left by an absent president with a racy account of some of the early meetings and members. Unfortunately neither of the last-mentioned talks were published and apparently no notes of those speeches have been preserved. In *Science* for December 22, 1933, is an article on the "Semi-Centennial of the American Society of Naturalists" which bears internal evidence of having been written by one of the older members, if not by a founder. Under these circumstances there is little if anything that I can say on this subject that is both new and true, but the long and eloquent gaps in the Secretaries' Records of the meetings offer a fruitful field for the scientific imagination.

Since history is long and time is fleeting I had thought to shorten my labors and diminish your distress by showing in a few lantern-slide projections some of the most significant events in the history of the society. And, as the pious but hurried college girl was said to have posted a typewritten prayer on the head of her bed to which she pointed when she jumped in at night, saying, "Lord, those are my sentiments," so I had thought that I could point to the lantern projection and say, "Behold the history of the American Society of Naturalists." But I found that history so extensive and, as you see, my lantern-slides so crowded and obscure that in this respect they resemble history itself and, therefore, even though you can not read a line, the pictures may well serve as a significant symbol, especially as you have to turn backward in order to see them.

As is well known to those who have read the *Records* of the society the initial step in its organization was taken by Professor S. F. Clarke, of Williams College. Mrs. Clarke has written me that when her husband went to Williams in 1881 as professor of natural history he soon felt the need of contact with colleagues in this field, and so, after much correspondence he issued the "Original Call" for a meeting to organize an American Society of Naturalists:

The intention is to have an annual meeting for the purpose of discussing topics of common interest, . . . as for example, museum interests; . . . methods of laboratory work; . . . new and valuable points in staining, mounting, cutting and preserving sections; systems of instruction; . . . the position which the observational sciences should hold in the college curriculum; the amount of natural sciences which should appear in college entrance examinations; the amount and character of such instruction in preparatory schools, etc. It is further believed that such a society could materially influence for the better the cause of science in America; that it would have a very healthful general effect, and could exert a strong influence in many directions where at present it seems to be very much needed. . . . The following gentlemen are interested in the enterprise and nearly all of them will be among those present:—

J. M. TYLER	G. MACLOSKIE
A. HYATT	W. LIBBEY
C. S. MINOT	H. F. OSBORN
A. S. PACKARD	W. B. SCOTT
S. H. SCUDDER	W. N. RICE
H. N. MARTIN	S. I. SMITH
W. T. SEDGWICK	S. F. CLARKE, *Secretary*

The initial meeting was held at Springfield, Mass., on April 10 and 11, 1883, and the society was organized under the name of "The American Society of Naturalists of the Eastern United States." Alpheus Hyatt was chosen president and S. F. Clarke, secretary. Later Professor Clarke was obliged to resign this office as he was going abroad, and Professor Minot (1902), in reviewing the early history of the society, said:

For some time it seemed doubtful whether the Society would get beyond its first meeting. I was then asked by Professor Hyatt to act as secretary and during the remainder of that year I carried on extensive correspondence with the professional naturalists of the country and nearly all of those who were invited accepted membership. It was then decided to hold a meeting in New York Dec. 27–28 of that same year.

There were 109 original members, 38 of whom attended the New York meeting, and 18 papers were presented, chiefly on laboratory methods and technique, such as cutting and staining microscopical sections, etc. If from our present point of view such topics are most uninspiring, it should be remembered that microtomes and histological stains were relatively new things in 1883 and

TABLE I.—AMERICAN SOCIETY OF NATURALISTS

Meetings	Presidents and Their Addresses	Discussions or Symposia
1883, Apr. 10–11, Springfield	Alpheus Hyatt	Organization of the Society.
1883, Dec. 27–28, New York	Alpheus Hyatt, The Business of the Naturalist	Methods and Technique.
1884, Dec. 29–30, Washington ...	Alpheus Hyatt	Methods and Technique.
1885, Dec. 29–30, Boston	G. C. Gilbert, Inculcation of Scientific Method	Methods and Technique.
1886, Dec. 28–30, Philadelphia ...	G. C. Gilbert, Special Processes of Research	Methods and Technique.
1887, Dec. 27–29, New Haven	Harrison Allen, The Inconstant in Biology	Science Teaching, Technique.
1888, Dec. 27–28, Baltimore	Harrison Allen, Study of the Human Cranium	Lab. and Lecture Instruction.
1889, Dec. 27–28, New York	G. L. Goodale	{ Science in the Schools. { Object of Scientific Gatherings
1890, Dec. 31, Boston	H. N. Martin, The Relations of Professor and Student	Inheritance of Acquired Characters.
1891, Dec. 29–30, Philadelphia ...	W. N. Rice, 25 Years of Scientific Progress	Definite *vs.* Fortuitous Variation.
1892, Dec. 28–29, Princeton	H. F. Osborn, The Humours of Paleontology	Marine Biological Laboratories.
1893, Dec. 27–28, New Haven	R. H. Chittenden, Recent Chemico-physical Discoveries regarding the Cell	Recent Discoveries Regarding the Cell.
1894, Dec. 27–28, Baltimore	C. S. Minot, The Work of the Naturalist in the World .	Environment as a Cause of Variation.
1895, Dec. 26–27, Philadelphia ...	E. D. Cope, The Formulation of the Nat. Sciences	{ Lab. Teaching of Large Classes. { Flora and Fauna of the Antarctic.
1896, Dec. 29–30, Boston	W. B. Scott, The Abuses of Speculation	The Inheritance of Acquired Characters.
1897, Dec. 28–29, Ithaca	C. O. Whitman, Functions and Features of a Biol. Sta.	The Biological Problems of To-Day.
1898, Dec. 29, New York	H. P. Bowditch	Advances in Methods of Teaching.
1899, Dec. 28, New Haven	W. G. Farlow, Scientific Organization in Universities .	Position of Universities regarding Investigation.
1900, Dec. 27–28, Baltimore	E. B. Wilson, Aims and Methods of Study in Natural History	Attitude of the States toward Scientific Investigation.
1901, Dec. 31–Jan. 1, 1902, Chicago	W. T. Sedgwick, Subjection of Science and Education to Propaganda	The Relation of the Am. Soc. Nat. to other Scientific Societies.
1902, Dec. 30–31, Washington ...	J. McK. Cattell, Homo Scientificus Americanus	How can Endowment be used most Effectively for Scientific Research?
1903, Dec. 29–30, St. Louis	Wm. Trelease, Critical Periods in the Life of a Naturalist	What Academic Degrees should be Given for Scientific Work?
1904, Dec. 28–29, Philadelphia ...	E. L. Mark	The Mutation Theory of Organic Evolution.
1906, Dec. 28, New York	C. B. Davenport, Cooperation in Science.	
1907, Dec. 31, Chicago	J. P. McMurrich, The Use of Continuing the Existence of this Society	Cooperation in Biological Research.

TABLE I.—(*Continued*)

Meetings			Presidents and Their Addresses	Discussions or Symposia
1908, Dec. 31,	Baltimore	.....	D. P. Penhallow, Functions and Organization of American Society of Naturalists.	
1909, Dec. 29,	Boston	.....	T. H. Morgan, Chance or Purpose in the Origin and Evolution of Adaptations	Fifty Years of Darwinism.
1910, Dec. 29–30,	Ithaca	.....	D. T. McDougal, Organic Responses	The Genotype.
1911, Dec. 28,	Princeton	.....	H. S. Jennings, Heredity and Personality	Relation of Genetics to Problems of Evolution.
1913, Jan. 2,	Cleveland	.....	E. G. Conklin, Heredity and Responsibility	Adaptation.
1913, Dec. 31,	Philadelphia	...	R. G. Harrison, Science and Practice	Biological Teaching & New Fields of Discovery.
1914, Dec. 31,	Philadelphia	...	S. F. Clarke, Early History of the Am. Soc. Nat.	The Value of Zoology to Humanity.
1915, Dec. 30,	Columbus	.....	F. R. Lillie, History of the Fertilization Problem	Advances in Fundamental Problems of Genetics.
1916, Dec. 29,	New York	.....	R. Pearl, The Selection Problem	Biology and National Existence.
1918, Jan. 1,	Pittsburgh	.....	G. H. Shull, The Genotype and Its Environment	Factors of Organic Evolution.
1918, Dec. 28,	Baltimore	.....	W. E. Castle.	
1919, Dec. 30,	Princeton	.....	E. M. East, Population	Some Relations of Biology to Human Welfare.
1920, Dec. 30,	Chicago	.....	J. Loeb	General Physiology.
1921, Dec. 29,	Toronto	.....	B. M. Davis, Species, Pure and Impure	Origin of Variations.
1922, Dec. 29,	Boston	.....	W. M. Wheeler, The Dry Rot of Academic Biology ...	{ Geographical Distribution. / Mendel-Galton Centenary.
1923, Dec. 29,	Cincinnati	.....	R. A. Emerson, Sex Expression in Plants	Morphogenesis.
1925, Jan. 1,	Washington	...	W. H. Howell, Theories of Inhibition	Growth.
1925, Dec. 28–30,	New Haven	....	C. H. Merriam, Beliefs of Calif. Indians about Animals	The Structure of Protoplasm.
1926, Dec. 29,	Philadelphia	...	J. A. Harris, Organization of Science	Quantitative Biology.
1927, Dec. 30,	Nashville	.....	C. E. McClung	Temperature and Life.
1928, Dec. 29,	New York	.....	H. H. Donaldson, The Bicentenary of the Norway Rat	The Neuro-Muscular System.
1930, Jan. 1,	Des Moines	....	G. H. Parker, Kim Kurmah, or What Are We About? .	Life and Radiation.
1931, Jan. 1,	Cleveland	.....	A. F. Blakeslee, $\left(A+\frac{hD}{2}\right)\cdot\left(Z-\frac{hD}{3}\right)$, or the Genetic Viewpoint	The Future of Man in the Light of His Past.
1931, Dec. 31,	New Orleans	...	S. J. Holmes, Changing Effects of Race Competition ..	Biology of Sex.
1932, Dec. 28–29,	Atlantic City	...	R. A. Gortner, Others	Heredity and Environment in Man.
1933, Dec. 30,	Boston	.....	B. E. Livingston, Environments	Biology and Society.

therefore timely even if tame. Methods and technique occupied the major part of the programs of the first six annual meetings. But by 1889 it seems probable that the members began to tire of this sort of laboratory spinach, for in that year they discussed a subject which might well be discussed at the present time, namely, "The Object of Scientific Gatherings." I am sorry that I do not know what conclusions were reached at that time, but it is significant that thereafter laboratory technique disappeared from the programs and that the discussions were on subjects of more general scientific and philosophic interest. At the very next meeting, that of 1890, the discussion was on "The Inheritance of Acquired Characters," thus opening a flood-gate of talk, which has deluged this and other biological societies ever since.

All branches of biology and geology were represented in the earlier membership and in the papers presented at the meetings. The second president of the society was a geologist, Grove K. Gilbert, the third an anatomist and physician, Harrison Allen. But in the year 1886 the Association of American Anatomists and that of American Physicians were organized; in 1887 the American Physiological Society and in 1888 the Geological Society of America. Thus within five years after the organization of the Naturalists it had given rise by gemmation or by fertilization to four other professional scientific societies; and in later years a numerous progeny has arisen. The American Morphological Society budded off in 1890 and metamorphosed into the American Society of Zoologists in 1903; the American Psychological Society was born in 1892, the Botanical Society of America in 1893, the American Bacteriological Society in 1899, the Ecological Society of America in 1915, the American Anthropological Society in 1923, the American Society of Parasitologists in 1924, the Genetics Society of America in 1930, and who knows how many other professional societies may trace their lineage back to this old grandmother of scientific societies. I know that there are some recent

upstarts who refuse to recognize this lineage and prefer to believe that their societies arose by spontaneous generation, but they would have as much trouble in proving this as biologists and theologians have had in other fields, or as some Nazis now have in disowning a non-Aryan grandmother.

TABLE II.—DATES OF FOUNDING OF AMERICAN PROFESSIONAL SOCIETIES AFFILIATED WITH THE AMERICAN SOCIETY OF NATURALISTS

1848	American Association for Advancement of Science, Sections F, G, H.
1883	American Society of Naturalists.
1886	Association of American Anatomists.
1887	American Physiological Society.
1888	Geological Society of America.
1890	American Morphological Society.
1892	American Psychological Association.
1893	Botanical Society of America.
1899	Society of American Bacteriologists.
1903	American Society of Zoologists.

INNOVATIONS INTRODUCED BY AMERICAN SOCIETY OF NATURALISTS
(According to C. S. MINOT, 1902)

1. Membership limited to professional scientific investigators.
2. Regular meetings in the Christmas vacations.
3. Discussions of the broader aspects of the natural sciences.
4. Affiliation and joint meetings with cognate societies.

According to Professor Minot (1902) this society is responsible for the following important innovations among American scientific societies: (1) Limitation of membership to scientific investigators; (2) holding the annual meetings during the Christmas recess of colleges and universities; (3) affiliation with cognate societies in the annual meetings and in support of scientific and public projects; (4) discussions and symposia on the broader aspects of the natural sciences. The first of these claims to priority may possibly be contested by some societies of greater age than ours. The American Association for the Advancement of Science was founded in 1848, the American Chemical Society in 1876, but neither of these limited membership strictly to professional scientists.

Our society first fixed upon the Christmas recess as the

time for its annual meeting, and this was followed by most of the societies which split off from it. Not until the Chicago meeting of 1901 did the American Association for the Advancement of Science adopt the plan of meeting regularly during that period, which was then named "Convocation Week"; since then our society and its numerous family have been graciously invited to meet at the same time and place along with the Association.

The American Society of Naturalists has always represented the more general aspects of the natural sciences. From the first its membership included zoologists, botanists, geologists, physiologists, bacteriologists, psychologists, anatomists, anthropologists, and, if for greater efficiency and effectiveness of treatment many branches of these sciences have now organized as separate bodies, it still remains true that the American Society of Naturalists serves an important function in the correlation and integration of these different societies.

Another important function which was initiated by this society is the practise of affiliating with other cognate societies in the annual meetings and in the support of important scientific and public projects. Indeed, if I am correct in claiming that most of our national biological and geological societies are the offspring of the American Society of Naturalists, this is a process of filiation as well as affiliation. Affiliations in meetings and programs were established with the physiological, anatomical and geological societies as soon as these were established, and at the time when the American Association for the Advancement of Science combined in 1901 with most of the national scientific societies there were ten societies affiliated with the Naturalists.

After the first few meetings of the Naturalists, which were largely devoted to the technique of laboratory and teaching, the discussions and most of the papers offered were of broad and fundamental interest. Among the notable discussions or symposia may be mentioned "The

Object of Scientific Gatherings" (1889), "The Inheritance of Acquired Characters" (1890, 1896), "Definite *vs.* Fortuitous Variations" (1891), "Flora and Fauna of the Antarctic" (1895), "Position of Universities Regarding Investigation" (1899), "Attitude of the State toward Scientific Investigation" (1900), "How Can Endowments be Used Most Effectively for Scientific Research?" (1902), "Cooperation in the Biological Sciences" (1907).

In order to more effectively serve this function of integration it was decided in 1908 that *Evolution* was the one most general and interesting topic common to all the natural sciences, and at the meeting of that year a "new temporary plan," proposed by Dr. T. H. Morgan, was adopted, providing that the study of evolution should be the policy of the society until otherwise ordered. Since then both evolution and genetics have continued to be the main topics of the papers and symposia, but with certain excursions into biometry, cytology, sex and society. In 1909 the symposium was on the appropriate topic "Fifty Years of Darwinism" and was published in a volume with that title. Some of the subsequent symposia were on "The Genotype" (1910), "Relation of Genetics to Problems of Evolution" (1911), "Adaptation" (1912), "The Value of Zoology to Humanity" (1914), "Biology and National Existence" (1916), "Factors of Organic Evolution" (1917), "Biology and Human Welfare" (1919), "Origin of Variations" (1921), "Geographical Distribution" and the "Galton-Mendel Centenary" (1922), "Morphogenesis" (1923), "Growth" (1924), "Structure of Protoplasm" (1925), "Quantitative Biology" (1926), "Temperature and Life" (1927), "The "Neuro-Muscular System" (1928), "Life and Radiation" (1929). In 1930 the topics shifted to the more directly human aspects of evolution with the discussion of "The Future of Man in the Light of His Past," and this direction was continued in the symposium of 1932 on "Heredity and Environment in Man," and in the notable symposium of this meeting of 1933 on "Biology and

Society." Many of these symposia were published in the American Naturalist, which was made the official medium of publication of the society at its third meeting (1885). These are certainly topics of broad and general interest, and it is safe to say that no one can measure the influence which these discussions have had upon American naturalists. At a meeting of some of the leading members of this society in the summer of 1932 it was decided that the society should by all means be continued and strengthened and should continue to represent the philosophical aspects of biology. Here is a field unoccupied by other societies and one of great educational value.

In this age of ever-increasing specialization there are many who look with amusement or disdain upon any attempt to stem this tide. To them natural history belongs to the Paleozoic era of culture, and even geology and biology are hopelessly out of date. Of course we must all recognize the necessity of specialization in science; indeed it is the means and method of all kinds of progress, and I shall not attempt to revive President Lowell's famous criticism of extreme specialization illustrated by that doctoral thesis to which he referred on "The Antennae of a Paleozoic Cockroach," and which was so humorously paraphrased by Professor Eigenmann.

But granting that specialization is a necessary factor in all progress and development it is also true that integration is an equally important factor. Indeed, as Professor Whitman used to insist, "specialization and cooperation are the companion principles of progress." Realization of this fundamental fact is now apparent among the leaders of all branches of science. It is seen in many recent books and addresses by mathematicians, physicists, chemists and biologists who are emphasizing the danger of regarding analysis as the sole aim and method of science, and of viewing mental abstractions and "isolates" as independent entities. Most of us realize that the older sciences of taxonomy and morphol-

ogy are mere fragments of biology and some of us think that highly specialized physiology and genetics are almost as lifeless as the old taxonomy and morphology. In short, the tendency of all specialized sciences is to isolate or abstract from the living being as a whole certain features or processes which have no really independent existence, nor when so isolated have they any *living* significance. They are studies of certain fragments of life, with the life left out. This method of analysis and isolation is necessary for effective treatment, but if it is to represent life it must be combined with methods of synthesis and integration; and we must never forget the interrelations of organisms to one another and to the entire environment. It is in maintaining these broader outlooks upon nature that the work of the naturalist is so much needed to-day.

The day is forever past when any one mind can even attempt a synthesis of all nature. There can never again be an Alexander Humboldt nor even another Georges Cuvier, Johannes Müller or Charles Darwin, and probably the specializations of the natural sciences have now gone so far that we can never again have great naturalists of the old type, such as Agassiz, Leidy, Cope and Hyatt. But if as individual investigators we must be specialists all the more do we need societies such as this that bring together these specialists in mutual cooperation and fellowship.

While the discussions or symposia of the Naturalists have always constituted the principal features of the annual meetings, the presidential addresses have often been notable contributions to science and civilization, and until very recent years a program of scientific papers was always offered. With the multiplication of more special societies the program of scientific papers has of late been omitted, but the presidential address at the annual dinner is happily continued. It is not possible to call attention to many of the notable presidential addresses, but I can not fail to mention the timely address of Professor

Sedgwick in 1901 on "The Subjection of Science and Education to Propaganda," the deep philosophy of Professor Jennings' address in 1911 on "Heredity and Personality," the wit and wisdom of Wheeler's address of 1922 on "The Dry Rot of Our Academic Biology."

Notable advances and projects which have been promoted by the Society of Naturalists are: (1) The support of science teaching in public and private secondary schools; (2) better organization of science teaching in colleges and universities; (3) better correlation of lecture and laboratory instruction; (4) assistance in establishing the *Journal of Morphology;* (5) support of the Naturalists table at the Marine Biological Laboratory at Woods Hole; (6) contributions toward the support of a research table at the Naples Zoological Station; (7) contributions of $500 to the library of the Marine Biological Laboratory and (8) of $200 to the support of the Concilium Bibliographicum; (9) promotion of Antarctic exploration; (10) support of proposals to create the Colorado Cliff-dwellers National Park, the Superior National Forest, the Quetico Provincial Park, the Everglades National Park, a biological station on the Great Lakes, the establishment of a National Health Service, and finally cooperation with the National Research Council in its section of Biology and Agriculture and with the Union of American Biological Societies in the establishment of *Biological Abstracts.*

Here is a record of intellectual stimulation and of practical achievement of which the society may well be proud. But perhaps no less important are the cultivation of social contacts among representatives of the different natural sciences. This is a *Society* of Naturalists, and I think that the "Object of Scientific Gatherings" is primarily social. Probably the success of our meetings depends more on social contacts than on scientific papers, perhaps more on the smoker and dinner than on the symposium or the address. Of course papers, symposia and addresses are necessary to stimulate scientific fellowship,

TABLE III.—AMERICAN SOCIETY OF NATURALISTS

Meetings	Some of the More Important Events and Transactions
1883 Springfield ..	Organization of American Society of Naturalists of Eastern United States.
1885 Boston	AMERICAN NATURALIST made Official Organ for Publication.
1886 New Haven .	Name of Society changed to American Society of Naturalists. Proposal of affiliation with the new Anatomical and Physiological Societies. Subscription of $60 to *Journal of Morphology.*
1889 New York ...	Conference with Physiological, Anatomical, Geological Societies.
1890 Boston	Report of Committee on Introduction of Science Teaching in Schools.
1891 Philadelphia..	Subscription of $100 to Naples Station. Request to Smithsonian Institution to establish a table at Naples Station.
1892 Princeton ...	Affiliation with Geologists, Physiologists, Anatomists, Morphologists.
1893 New Haven .	Meeting with Morphologists and Physiologists. $500 voted toward Endowment of Library at Marine Biological Laboratory.
1896 Boston	Meeting with Anatomists, Morphologists, Physiologists, Psychologists. Report of Committee on Antarctic Exploration.
1897 Ithaca	Meeting with 7 affiliated societies. Appropriation of $50 for support of "Naturalists Table" at Marine Biological Laboratory. Vain appeal to President McKinley to appoint a scientist as Fish Commissioner.
1898 New York ...	Meeting with 8 affiliated societies.
1900 Baltimore ...	Meeting with 8 affiliated societies. Approval of Regional Branches of Am. Soc. Nat.
1901 Chicago	Meeting with 8 affiliated societies. Formation of Central Branch of Am. Soc. Nat.
1902 Washington .	Initiation by A.A.A.S. of "Convocation Week." Meeting with 10 affiliated societies. Continuation of subscription to Naples Station and to Marine Biol. Lab'y. Recommendation of establishment of Biol. Station on Great Lakes by United States Fish Commission.
1908 Baltimore ...	Adoption of "New Temporary Plan that Study of Evolution be General Policy of the Society, unless otherwise ordered."
1913 Philadelphia..	Abolition of Division of Society into Eastern and Central Branches.
1915 Columbus ...	Resolution favoring Reform in Methods of Securing Expert Opinion in Judicial Procedure, also favoring Centigrade Scale of Temperature Measurement. Appropriation of $200 to Concilium Bibliographicum.
1916 New York ...	Working plan of Society to be: (1) Annual Dinner with President's Address, (2) Research Papers on Problems of Organic Evolution, (3) Symposium on Timely Topic.
1918 Pittsburgh ..	Election of 2 representatives to Committee on Botanical Abstracts.
1920 Toronto	Election of President and Secretary to Inter-Society Council to formulate plan of Federation of Biological Societies.
1922 Boston	Voted to join Union of American Biological Societies for year 1923.
1923 Cincinnati ..	Membership in Union of Am. Biol. Soc. to be continued until rescinded by Society.
1928 New York ...	Approval of establishment of Superior Nat'l. Forest & Quetico Provincial Park.
1930 Des Moines ..	Appointment of Committee on Policy to Study Relations of American Society of Naturalists to other biological societies.
1931 Cleveland ...	Approval of establishment of Tropical Everglades National Park. Approval of report of Committee on Policy recommending: (1) Continuance of Society and centering of attention on problems of organic evolution. (2) Selection of President with especial reference to annual address and discussion. (3) Vice-President to organize Symposium. (4) Society to sponsor annual Biologists' Smoker. (5) President's address and symposium papers to be printed and circulated to members. (6) Distinguished foreigners to be invited to address Society. (7) Society to assist in publishing material of wide biological interest. (8) Qualifications for membership to include (a) high order of research, (b) wide philosophical interest. (9) Membership to be limited to approximately 600. (10) Society to serve as a nucleus for biological meetings at Easter or when not meeting with A.A.A.S.

but so far as they are merely contributions to knowledge they are distinctly inferior to the printed page and, if long and detailed, are a weariness to the flesh, while there is no substitute for fellowship. The addresses and papers which we remember are those that reveal human personality; those which stir emotions of humor, imagination, adventure, even conflict. More things are wrought by fun than this world dreams of; folly goes down under the arrows of wit more quickly than under the broadsides of erudition; and what can take the place of the spoken word in stimulating the imagination and the spirit of adventure? Even conflict, within certain bounds, is a wholesome and desirable part of scientific meetings. More fun and fight, and less solemn dullness regarding dry facts, concerning which no one would ever drop a tear or a cuss word, would crowd our meetings and keep the members awake. Whatever may be true of other scientific bodies, no society of naturalists can long survive on a diet of mathematical, chemical or genetical formulae, or of curves, graphs and tables, any more than on fixing, sectioning, staining and mounting sections, with which pabulum this society began. These things are necessary tools of science and have their proper place in detailed papers, but society meetings must have some human interest, some mixture of emotion with reason, of imagination with verification, of poetry with truth. In short, such meetings should aim at humanizing knowledge.

Of course, in the search for truth scientists must not be guided by emotion and, as far as possible, must avoid wishful thinking and personal animus. Probably no other sources of error are more serious than these, and in general the more emotion any research reveals the less confidence it inspires. But on the other hand it is the love of truth, the feeling of its value, the stimulus of imagination and the hope of achievement that inspire the scientific worker.

Knowledge is ever advancing, and many of the subjects

which were discussed with so much fervor fifty years ago are almost forgotten to-day, but the fervor and human emotions of fifty or five hundred years ago remain relatively unchanged. Many of the old programs of scientific societies have the neglected and futile aspect of those pitiful piles of old books on sidewalk stands that beg for attention and a purchaser at five or ten cents a volume. They induce solemn thoughts on the transitory character of all knowledge.

> Our little systems have their day,
> They have their day and cease to be.

But in general the emotions that animated our predecessors animate us, they are perennial, whereas knowledge is annual or ephemeral. Members of scientific societies, no less than alumni at their reunions, forget the knowledge so laboriously imparted and recall vivid personalities.

The older naturalists were not ashamed, as so many of us are, to reveal the fact that they had human emotions. Many of them were artists, poets and sometimes first-class fighting men. I well remember the first meeting of the society which I attended in 1895, when Cope, who was president that year, made an address which was full of fun and fight and the exposure of shams, but the printed form of that address, which appeared some time later, had undergone a sad but necessary scientific revision. I am not pleading for a resumption of those bitter personal quarrels which created lasting enmities, such as the fight between Marsh and Cope, or Lankester and Fol, or Bateson and Pearson, which were often animated by personal animosity or a mad rush for priority, and which usually generated more heat than light, but rather for that frank expression of opinion among friends which stimulates wits, as steel sharpeneth steel. Our society has done much to prevent the former and promote the latter and thus to preserve social amenities among scientists.

The daughter of Professor J. S. Kingsley, who was one of the original members, has sent me a page from her father's unpublished recollections which indicates that he believed that the principal function of scientific meetings was the opportunity afforded for informal social contacts. Kingsley wrote:

> In my earlier years I listened religiously to all of the papers presented at the meetings, understanding most of those which dealt with my subjects and trying to assimilate something from the rest. As years passed those which especially interested me were relatively fewer, largely because of the development of zoology in every direction and for some I lacked the necessary chemical and physical bases necessary to comprehend them. So I neglected some because they were too abstruse, some (like those on taxonomy) because of their tediousness and lack of any inspiration. . . . In later years I have listened to few of the disquisitions; instead I have walked the corridors, finding others like myself in feeling that these chance contacts and the ensuing conversations were more helpful and inspiring than most of the papers.

Some of the discussions to which Kingsley refers were memorable not only for their lack of inspiration but also for the pain they caused the audience. Even at the safe distance of more than thirty years, who that heard them can forget the futilities of those repeated discussions of "The Inheritance of Acquired Characters"? I heard this subject discussed before this society, at the Boston meeting of 1896. Some of the speakers were most interesting if unconvincing, especially so Cope and Wm. James, but some were mortally long and dull. In the night following this discussion Watase, the Japanese zoologist, was heard to mutter in his sleep, "O damn ———," naming the speaker who had kept him so long from his dinner, while many escaped furtively from the back of the hall and others from the front seats by having apparent nose bleed. All long-suffering audiences are ready to say with Kipling's Tramp Royal:

> God bless the world;
> Except when very long I've found things good.

The fiftieth anniversary of the founding of the American Society of Naturalists finds this body a relatively

small one amid the great aggregation of scientific societies, most of which have arisen since its founding, but it still occupies an important and unique position among American scientific societies. It is still the only national society which attempts to bring together the representatives of all the natural sciences for the discussion of the broader philosophical aspects of those sciences and for the promotion of scientific and public enterprises which fall within the field of those sciences. Unfortunately, our geological, anatomical and physiological offspring rarely come back to their old home hearth, but the door is always open to them, and if they do not affiliate with us as societies they are nevertheless represented in our meetings by some of their leading members. Among these, three of the founders of this society, namely, Professors Gage, Osborn and Scott, are with us to-night to take part in this semi-centennial celebration, and with them is another, who if not strictly a founder of this society, is the editor who publishes its symposia and addresses and who is probably the chief promoter of science in America—Professor J. McKeen Cattell. On you and the society which you have founded and promoted we invoke Rip Van Winkle's blessing: "May you all live long and prosper."

THE NUCLEUS–PLASMA PROBLEM. II

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THE EVIDENCE FROM RECIPROCAL HYBRIDS

The observations from which the most plausible arguments in favor of a plasmon have come are those where differences in reciprocal hybrids have been found. They are relatively numerous and are so varied in nature that it is convenient to divide them into two groups: the one, containing those cases concerned with the development of certain plastid characters, where there appears to be a complete independence of nuclear control; the other, including those cases where the nucleus and the plasma seem to play supporting rôles.

Plastid inheritance. It is but natural to seek a non-nuclear vehicle of heredity in the plastids. They are found in all groups of plants, except certain orders of parasites; and they are readily distinguished visually and chemically. Unfortunately, however, our knowledge of their origin and behavior is very incomplete. For example, it is customary to call all colorless plastids, leucoplasts; yet there is clear evidence that apparently identical leucoplasts may develop either into amyloplasts or chromoplasts, thus indicating that there is metamorphosis or that several juvenile types are being grouped together. And the two kinds of plastids mentioned are merely selections from among those producing various hydrocarbons, or carbohydrates, or chlorophylls, or oils. Again, although there is definite proof that the plastids of certain lower plant forms undergo division and are allotted to daughter cells with some precision, there is no unanimity of opinion supporting Schlimper's view that plastids never arise *de novo*. The confusion is greater in the angiosperms, where most of the genetic evidence has been obtained, than elsewhere; for the cells of angiosperms contain numerous plastids of various kinds, while

such lower forms as Anthoceros and Coleochoete have but one individual to a cell.

The trend of opinion concerning the angiosperm plastids, in which we are interested here, is that they are developed from minute cytoplasmic primordia, and that these primordia reproduce by division. One may term these primordia *proplastids,* with Randolph, and thus evade definition; or one may identify them with the chondriosomes, as do Lewitsky, Guillermond and others. Such distinctions are immaterial. From the morphological and the physiological points of view, it would also appear to be immaterial whether one believes that the chondriosomes are cell products or organic symbionts similar to bacteria; but to the geneticist the distinction is important. It should be mentioned, therefore, that the latter theory, held by Portier and Wallin, should be given serious consideration, since it is susceptible of proof through culture *in vitro.* The criticisms offered against it by the members of the micro-dissection school, while grave, are not wholly destructive.

Genetic analyses of plastid differences are numerous. At least one hundred cases have been investigated where there are simple color differences presumably indicative of the production or non-production of carotin, xanthophyll, and related hydrocarbons. More than one hundred cases have been analyzed where there are contrasting phases in reserve materials, such as starch, sugar, dextrin, etc. Without exception, the controls proved to be nuclear, for all of them exhibited clear and definite Mendelian inheritance.

Similar conclusions may be drawn for the great majority of the cases examined where the contrasting characters are due to chloroplast activity. Over four hundred specific instances have been studied, distributed over nearly fifty species. With the exception of about forty examples, Mendelian inheritance governs. Generally, the control is marked at a single locus; but several more complex situations have been discovered where two,

or even three, genes are concerned. In about a score of studies, linkage has been found with other known genes.

Certain exceptional cases remain, however, where inheritance is usually through the mother; and it is important to observe that all these cases, with the possible exception of the two found in maize and investigated by Anderson (1923) and by Demerec (1927), are examples of variation of a similar type, the variegation known as *Status albomaculatus.*

The first work on this type of inheritance was that of Correns (1909) on *Mirabilis jalapa.* From that time until his death, Correns studied the heredity of *albomaculata* variegation in Arabis, Aubretia, Mesembryanthemum and Urtica (1919), and in Stellaria, Taraxacum, Hieracium and Senecio (1922), in such a careful and critical manner that he became, and remained, the leading authority on the subject. He brought his results together in 1927 and presented them at the Fifth International Congress of Genetics, held in Berlin (Correns, 1928). Additional cases have been described and studied by Anderson (1923) in Zea, by Baur (1907, 1911) in Antirrhinum, by Brozek (1923) in Mimulus, by Clausen (1927) in Viola, by Dahlgren (1921) in Barbaraea, by Demerec (1927) in Zea, by Gregory (1915) in Primula, by Shull (1914) in Melandrium and by Sprenger (1916, see Wellensiek, 1925) in Pisum. Other observations have been reported[3] with a more or less complete analysis appended; but these papers represent a random sample.

Inheritance in the *albomaculata* plants is through the mother only. Green branches yield green progeny, white branches yield white progeny, and variegated branches yield variegated green and white progeny—all without reference to the origin of the pollen. In addition, there is one example where the variegated plants produce only variegated progeny, irrespective of the pollen used. This

[3] Since this paper was written, de Haan's monograph (1933) has appeared. In it the reader will find a complete list of the literature on chlorophyll deficiency. De Haan's work, however, is a compilation rather than a critique.

is the Humulus variegation reported by Winge (1919). There is also an odd case observed by Terao (1918), where variegated plants of Glycine gave only green progeny.

Finally, one may add a few instances, apparently belonging to the *albomaculata* category, where the inheritance is biparental, yet not Mendelian. The type is the periclinal chimera *Pelargonium zonale,* investigated by Baur (1909, 1919), by Noack (1922, 1924, 1925, 1931) and by Roth (1927), where the results are complicated by the existence of two somatically distinct layers of tissue. There is a one-celled or two-celled envelope of white, surrounding a core of green; or the reverse. Essentially similar observations have been made on Oenothera (De Vries, 1903; Stomps, 1919), Amaranthus (Chapin, 1914), Erodium (Scherz, 1927), Hypericum (Correns, 1931) and Borrago (Noack, 1931). An example, cited by Ikeno (1917), and not a chimera, is now regarded by him as infectious chlorosis (Demerec, 1927).

The facts here are not in question, except in unimportant details, if one keeps in mind the condition of the growing point. They have been summarized accurately by Demerec (1927) as follows: (1) *Zonale* plants selfed or intercrossed gave only white progeny. (2) When crossed with green plants, they yielded white, variegated, and green plants in varying proportions. In Baur's experience, reciprocal crosses were identical; in Noack's experience, a larger proportion of variegated plants were obtained when *zonale* was the female parent. (3) Green F_1 plants, as well as green patches of variegated plants, when selfed or crossed, behaved as normal green plants. (4) In crosses with green, different *zonale* plants transmitted the variegation in different proportions and intensity. Baur found that the seedlings only were variegated, mature leaves being green or white, sectorial or periclinal chimeras; while Roth found that the variegation persisted.

Baur's own interpretation of these results is that in-

heritance is through the plastids, some of which are brought in through the generative nucleus. Noack, on the other hand, criticized the idea that the plastids themselves are genetic agents, on morphological grounds, since small bracts and large leaves are similar in type. He believes that the cells of the meristem are in a labile state which may result in the origin of green or of white cells, the change being irreversible. The condition, he thinks, is not one of true heredity but rather of disease transfer.

Other interpretations, applying particularly to the Pelargonium category, have not been wanting. Bateson (1919) suggested somatic segregation as a possible explanation of periclinal chimeras in general. But such an interpretation meets with insuperable theoretical difficulties, even where ordinary periclinal chimeras are concerned, though it does account for certain bud variations which may occasionally produce them. One of these obstacles, when dealing with chlorophyll deficiency, is the presence of maternally inherited variegation in fern gametophytes (I. Anderson-Kottö, 1931).

Demerec (1927) has proposed the hypothesis, though he does not believe it to be the most probable one, that some of these conditions, at least, are caused by mutable Mendelian genes. He points out that the results obtained on *Pelargonium zonale* are to be expected if the *zonale* character is determined by a dominant mutable gene which becomes mutable (to green) in crosses with green, or when the plant is heterozygous for green. The idea obtains some support from Emerson's (1922) work on the variegated pericarp of maize, and from his own studies on the "miniature" and the "reddish" mutants of *Drosophila virilis*. These are cases where apparently constant genes become highly mutable in the presence of certain other genes. It may also be argued that Anderson's (1923) discovery that like types of conditioning tend to occur in patches on the ear in his case of maternally inherited chlorophyll variegation of maize, is a supporting phenomenon.

Mendelian explanations have also been suggested for the inheritance of the *albomaculata* condition, where chimeras are not in question. Sturtevant (1915) proposed balanced lethals. Stomps (1919) used the conception of a "panlabile" gene, an idea presumably similar to that which was given in more detail, later, by Demerec. Collins (1922), to explain observations on Chlorophytum, brought in the concept of heterosis.

The facts, however, are not easily explained by orthodox Mendelism, as suggested by Sturtevant, since the segregating forms issue in highly variable proportions that are hardly compatible with known gene ratios, even when allowance is made for translocations giving lethal combinations; and the hypothesis of highly mutable genes is itself a makeshift resting on dubious grounds.

At present, there would seem to be a logical choice only between the theory that there are two types of plastids, as assumed by Gregory (1915), and the theory that there is a diseased cytoplasm affecting plastid development (Correns, 1909, 1928).

Gregory proposed his theory to account for the condition found in *Primula sinensis albomaculata*. It assumes the existence of normal and of chlorotic chloroplasts in the same cell. These chloroplasts are supposed to be able to reproduce their type and possibly to have differential rates of reproduction. The theory has been supported by Winge (1919) and by Chittenden (1925).

The hypothesis of Correns, however, appears to me to be the more plausible. There are several reasons for this choice. Chief among them is that from what we know of all other types of determination of plastid qualities, we should expect that the inheritance of green and of white plastids, considered as morphological entities, should be controlled by the nucleus. And if we assume that the white plastids are themselves diseased, rather than conditioned by a diseased cytoplasm, the facts are less easily harmonized with the data of pathology.

Correns' hypothesis is the acme of simplicity except

in one respect. It assumes that the cytoplasm may exist either in a healthy or a diseased condition, the plastids being prevented from functioning normally when in cytoplasm of the diseased type. It is thought, and this is the one complication, that the embryonic cells are in a state of balance and may give rise, *by chance,* either to healthy or to diseased cells. The time of origin of either type determines the size of the area of white or of green tissue, since it is assumed (an assumption apparently supported by the facts) that once a non-meristematic cell has its condition fixed, there is no reversion to the other type. When, as in *Humulus japonicus* (Winge, 1916), the mosaics crossed with normals reproduce themselves only instead of giving rise to pure green or to pure white plants, it is supposed that the labile condition, usually exhibited exclusively by meristematic cells, is characteristic of all cells.

This hypothesis is the simplest yet proposed, though it does not give us a complete picture of the situation. If accepted, it removes *albomaculata* as the one outstanding exception to Mendelian heredity. It becomes merely an illustration of the behavior of an active, parasitic agent which can not, as filterable viruses appear to do, pass through living membranes. Perhaps future investigations will determine just how its effects are produced. It is possible that the "chance" of Correns, which directs the receipt of healthy or of diseased cytoplasm from the labile embryonic cells, is the manifestation of an immunological phenomenon. It may be that the embryonic cells are bad incubators where intense cell activity prevents active behavior of the infective agent, and where the length of time elapsing between cell divisions determines whether labile cells (unaffected), green cells (the agent killed) or white cells (the agent dominant) are produced. Or, it is possible that antibodies are formed; and that the relative quantity of antibodies and of the infective agent received by the daughter cells (and again a time relation may be involved) determines whether health or disease prevails.

It may be asked whether analogies exist which render the disease hypothesis plausible. There are, in fact, many such analogies, showing that inactive chemicals (Sudan red), active chemicals (antigens), parasites and symbionts, may be transferred from cell to cell and thus give an illusion of hereditary transmission.

Several investigations (see Ratner, 1927) have given definite proof of antigens passing the membranes which separate the maternal circulatory system from the fetal system in mammals. The embryos react and produce antibodies. Evidence is lacking that such reactions are common in mammals or that analogous reactions occur in other animals and plants. But the possibility remains that they may occur in any of the great organic groups, and that the antigen-antibody reactions may produce fleeting morphological changes.

The evidence is more extensive that parasites can be carried in the maternal cytoplasm and will produce definite effects, generation after generation, through reinfection. Noteworthy among these agents are the so-called filterable viruses which are so widely distributed throughout the angiosperms. Comparable examples are known in insects and in mammals. In addition, several instances have been discovered among mammals where identifiable parasites of larger size, such as protozoa, are carried in the cytoplasm and reinfect successive generations.

Finally, it should be noted that a large number of intracellular symbionts have been described. It will be sufficient to mention the algae or alga-like symbionts of the lichens and of various hydras, and the fungus symbionts of numerous insects.

Thus there are several types of phenomena where there is direct transfer, from cell to cell, of alien matter capable of producing morphological changes. It is not to be supposed that modern biologists will cite such instances, when recognized, as examples of heredity. But since an earlier generation of students used them, before their

cause was discovered, to support arguments on the inheritance of acquired characters, it is well to be cautious in citing similar, though less obvious, cases as being illustrative of non-Mendelian heredity.

It should be noted, perhaps, before closing this part of the discussion, that Anderson (1923) believed the infection hypothesis to be an improbable interpretation of the facts in the maize case which he studied. His reasons were: (1) The character did not spread to cells other than those marked out by cell multiplication. (2) There was no repetition of the condition in contiguous cultures. (3) The only means of transmission was through striped plants, and the affected progeny produced were very weak. The same remarks would apply to the other examples belonging to this category; but, in view of the fact that the theory of Correns evidently presupposes an intra-cellular parasite capable of dissemination only at cell division—a type known to exist—the objections are not to be taken seriously.

Before leaving this particular phase of the subject, it may be well to mention that several instances of chlorophyll deficiency have been observed when two green-leaved species have been crossed together, and this phenomenon has been ascribed to the action of an independent plasmon (Renner, 1929). It is thought that the plastids of one species do not develop properly when under the influence of the genes of the other species. While this conclusion is not necessarily incorrect, it should be pointed out that there are other explanations. In the twin hybrids of Oenothera, arising from crosses between green forms, the progeny exhibit several different types of abnormal chlorophyll development. But there is nothing in the facts, so far as I can see, which prevents one from assuming that this is the resultant of gene action. Certainly the etiolated hybrids described by Mangelsdorf and East (1927) in *Fragaria vesca* × *F. elatior,* and in *Fragaria vesca* × *Potentilla nepalensis* are more simply interpreted as crosses where the whole

machine functions poorly; that is to say, the hybrids are weak and chlorotic. This interpretation also holds for *Pelargonium denticulatum* × *P. filicifolium* (Smith, 1915) and for *Linum hirsutum* × *L. viscosum* (Fischbach, 1933), in my opinion. In *Geranium Bohemicum* × *G. deprehensum* (Dahlgren, 1923, 1925), in *Campanula medium* × *C. mirabilis* (Correns, 1928), in the Hypericum crosses of Farenholtz (1927) and Noack (1931), and perhaps in a few others, where unexplained reciprocal differences are in evidence, one may as reasonably accept tentatively the idea of cytoplasmic action. But it should not be forgotten that this explanation can not be held as satisfactory in the absence of cytological control. Moreover, there is no evidence whatever that the cytoplasmic influence is that of a plasmon in the sense of Von Wettstein. The fact is simply that plastids which presumably come from the mother plant do not function well when under the influence of the hybrid nucleus.

Non-plastid inheritance. Differences in reciprocal hybrids which have no connection with the plastids may now be considered. Such data are fairly numerous; but nearly all the observations which have critical value have been made upon plants.

In animals, apart from the late influence of maternal genes, which has already been mentioned, inter-varietal crosses seldom show reciprocal differences. Those which do, yield to explanations which do not require an independent plasmon, as for example, the duck hybrids reported by Phillips (1912, 1914), where development is influenced by the size of the egg, or the Lymantria crosses of Goldschmidt, where nuclear influence gives a complicated type of sex determination. Species crosses, on the other hand, where reciprocal differences might be expected, present serious difficulties. When there is failure in one direction, this failure may logically be ascribed to the cytoplasm; but one must not forget that psychological restrictions in mating, or physiological restrictions (such as a difference in the period of gestation ascribable

to maternal genes) may equally logically be given as an explanation. Where both crosses are possible, the hybrids are too often sterile, thus making critical tests impossible. Moreover, much that we possess as evidence of differences in reciprocal crosses is mere tradition. For example, though it is commonly thought that several mammalian reciprocals are unlike (Lang, 1914), no statistical proof has been offered, even in the most notorious case—that of the mule and the hinny.

A considerable amount of legitimate zoological data remains, however. It comes, in the main, from experiments on echinoderms and on fishes, where crosses between distant species are ordinarily obtained without difficulty, and where extraordinary reciprocal differences are observed. But most of these differences are readily explained as being due to chromosome eliminations, and most of the remainder are examples of control by the maternal nucleus in early stages of differentiation. Naturally, one can not deny the possibility that a plasmon is also acting; the difficulty is that its existence can not be established without very complete genetic knowledge of the parental types used in the experiments.

Since the requisite knowledge for a satisfactory experimental set-up is virtually impossible on such forms, and bisexuality is a serious complication in any event, it seems more practicable to restrict the investigation of the plasmon to plant material, except where the animal material holds special advantages. I mean, by this remark, that the observations of Kühn (1927)[4] on reciprocal differences in Habrobracon, and the suggestion of Little (1933)[5] that tumor incidence in certain strains of mice is influenced by the cytoplasm, may well be followed up, since genetic knowledge of these forms is considerable.

In plants there are numerous examples of differences

[4] Kühn feels that in order to account for certain differences in pigmentation, it is necessary to postulate plasma influence in addition to gene differences.

[5] Here the direct transfer of an alien exciting agent is not excluded.

in seed size influencing growth-rate, a few examples of late influence of maternal genes, and several examples of reciprocal differences manifested in later stages of development. Many of the latter, among them being observations on Aquilegia (Skalinska, 1928; Anderson, unpub.) and on Digitalis (Hill, 1925, 1929; Jones, 1912, 1929; Michaelis, 1931), have not been studied sufficiently to give them critical value. Moreover, they are frequently complicated by induced parthenogenesis, a phenomenon which I also have observed many times. But there are five pieces of evidence which should be considered with care. These are: the work on gyno-dioecious plants, the observations on male sterility, the investigations on Epilobium, the investigations on Vicia, and the researches on mosses.

The extensive observations on gyno-dioecious plants are largely due to Correns (1908, 1916, 1928), although several other workers have amassed corroboratory data. The facts are as follows, taking the observations on *Satureia hortensis* and *Cirsium oleraceum* as typical. Both the female plants and the hermaphroditic plants reproduce the sex class of the mother exclusively, though the females obviously can receive only the pollen of hermaphrodites. The situation is the same even when female plants of *Cirsium oleraceum* are successively backcrossed with pollen from hermaphroditic plants of *Cirsium canum*. The autosomes segregate normally, pollen abortion is low, fruitfulness is excellent and the chromosome equipment of *C. oleraceum* is gradually replaced by that of *C. canum*, if one may judge the situation by the behavior of other characters; yet the sex still follows the mother.

It is not easy to offer a chromosomal explanation for these results. No theory of genic balance can possibly hold; and, in the absence of class elimination either in the gamete or the zygote, all hypotheses involving specific gene determiners must be rejected, *unless* one postulates selective fertilization.

The plasmon theory, on the other hand, which was suggested first by Von Wettstein (1924), is simple and plausible. It merely assumes that the cytoplasm of the female plants carries some substance which inhibits the development of the male organs, and that the essential chemistry of this plasmon is uninfluenced by nuclear substitutions.

Bateson and Gairdner, in 1921, discovered a case of male sterility which was later found to be due to cytoplasmic interaction with nuclear factors (Chittenden and Pellew, 1927). When a certain tall flax was crossed with a procumbent flax, the descendants exhibited normal fertility. When the reciprocal cross was made, however, the procumbent flax being used as the mother, male steriles were found in the F_2 generation in a 3:1 ratio.

East (1932) found a similar situation in crosses between the self-fertile species *Nicotiana Langsdorffii* and the self-sterile species *N. Sanderae.* When homozygous S factors (genes for self-sterility) were present in cytoplasm derived from *N. Langsdorffii,* all plants were male sterile. In addition, several other characters appeared to be inhibited in their development if the genes (homozygous) primarily responsible for their development were derived from one species and were in the cytoplasm of the other species. Two generations of backcrosses were reported, thus permitting a large amount of chromosome substitution, since both species contain but nine pairs of chromosomes. Yet there was apparently no change in the situation. The plants continued to be male sterile when homozygous S factors were present if the cytoplasm had been derived originally from *N. Langsdorffii.* The experiments are being continued.

The most extensive piece of work on male sterility of this type has been carried out by Rhoades (1933). A male sterile maize plant was found in a culture arising from seed collected by R. A. Emerson and F. D. Richey in Peru. Crossed to an unrelated type, a population of 45 male steriles resulted. Appropriate experiments showed that the condition was not carried by the pollen

of partially sterile plants, but, on the contrary, was transmitted solely through the mother. An experiment was then planned by which each of the ten chromosomes of the male sterile biotype could be replaced by marked chromosomes known to be free from sterility-producing genes. The final result of this huge investigation was to show that male sterility was not linked with any of the genes in the various linkage groups. It was also found that the distribution of male-steriles and of normal seed on the cob was such as to lend no support to any conception of a cytoplasmic hereditary factor segregating somatically before megasporogenesis.

Since the publication of this paper, Rhoades has accumulated important evidence from five generations of backcrosses. Successive backcrosses have yielded male steriles in each generation; but after the third backcross, if I have understood Rhoades correctly, an increased proportion of plants having functional pollen is produced. At all events, there is an indication that changes are occurring, though there is no critical proof that these changes are due to the action of novel nuclear combinations. It is possible, however, that such is the case, since it was not feasible to control all portions of each chromosome in the chromosome replacement experiment and thus to be absolutely certain of the nuclear situation involved.

The reciprocal differences that have been investigated most extensively are those involving two species of Epilobium, *E. roseum* and *E. hirsutum* (=*E. parviflorum*). The genus Epilobium is closely related to the genus Oenothera, a fact which makes the geneticist expect that cytological abnormalities will be found. But, in so far as the facts are known, there is nothing extraordinary or peculiar in the chromosome behavior of the species. All the species thus far investigated (Håkansson, 1924; Schwemmle, 1924; Michaelis, 1925) have been found to have 9 pairs of chromosomes which show normal pairing and segregation, though there is room for more detailed

study. Hybrid behavior, where the production of hybrids is possible, is also of the usual type, except where *E. parviflorum* and *E. hirsutum* are concerned.

E. hirsutum is a European species belonging to the subgenus Lysimachion; *E. luteum* is an American species and is the sole representative of the subgenus Chrysonerion. Their crossing behavior has been studied by Geith (1924), Lehmann (1918, 1925, 1928, 1931), Michaelis (1925, 1926, 1928, 1929, 1931, 1932, 1933), Renner and Kupper (1921), Lehmann and Schwemmle (1927) and Schwemmle (1932). There is no essential difference of opinion about the facts. Reciprocal crosses within the species *E. hirsutum,* which does not vary much, are similar, and show normal segregation. Similarly, reciprocal crosses between the varieties of *E. roseum,* of which there are a number, are similar, and behave in the ordinary way. But reciprocal crosses between *E. hirsutum* and *E. roseum* are dissimilar, the dissimilarities showing in habit of growth, size of the vegetative organs, size of the petals, development of the anthers and in the grade of fertility. In the combination *E. hirsutum* $\times$ *E. roseum,* the petals and anthers are reduced, and the plants are almost completely sterile; in the combination *E. roseum* $\times$ *E. hirsutum,* the petals and anthers are well developed and the plants are fairly fertile. Different varieties of *E. roseum,* however, when crossed with *E. hirsutum,* produce F_1 plants exhibiting different degrees of sterility.

Renner and Kupper, and Michaelis, ably supported by Von Wettstein, have interpreted these observations by the assumption that the plasmon has an influence which is independent of the nucleus. The genes of *E. roseum* are supposed to develop very badly when in combination with the plasmon of *E. hirsutum,* although the genes of *E. hirsutum* can develop fairly well when the substratum is the cytoplasm of *E. roseum.*

With the substance of this interpretation there is no quarrel. Lehmann and Schwemmle agree that the end results here described are due to the interaction of differ-

ent cytoplasms on a given hybrid nuclear complex. The hybrid nucleus functions better in the *E. roseum* cytoplasm than it does in the *E. hirsutum* cytoplasm. Where Lehmann and his followers part company with Renner and his followers is on the question of whether the plasmon is a physical vehicle of heredity independent of the nucleus. Lehmann, on the basis of his experience with crosses between the various forms of *E. roseum* and with crosses between these varieties and *E. hirsutum,* feels that the facts are susceptible of a simple interpretation by postulating (a) that different nuclear constitutions react variously in different specific cytoplasms and (b) that each nuclear combination influences the production of a specific type of cytoplasm.

Unfortunately, there are no critical data which enable one to decide which of these two opinions is correct. Renner offers no proof of an independent plasmon, and Lehmann offers a plausible explanation without one. It should be noted, however, that the recent experiments of Michaelis (1933), which might have been expected to furnish critical evidence and which he offers as critical evidence in favor of the ideas of Renner, are really more favorable to those of Lehmann.

Michaelis saw clearly that the most substantial proof of a plasmon would be to find similar results in each generation of a series of backcrosses of *E. roseum* × *E. hirsutum* with *E. hirsutum,* since the nuclear constitution would change in each generation. Accordingly, it was planned to make a succession of backcrosses on the original reciprocal hybrids. Unfortunately, it was very difficult to carry out the experiment because the plants were so sterile.

The F_1 plants of the combination *E. hirsutum* × *E. luteum* were backcrossed many times with pollen of *E. luteum* throughout several growing seasons; but only a few plants were obtained. These plants were even more sterile than those of the F_1 generation. The anthers were more reduced, the tissue was more degenerate, and

in various other ways the plants showed restricted development. In several cases, they did not even come to blossom. Continued attempts to obtain a second backcross generation were failures except in the case of one individual which finally produced a few shrunken seeds. From these seeds 40 abnormal seedlings were obtained, and these did not go further than the seedling stage.

The F_1 combination *E. luteum* × *E. hirsutum*, when backcrossed with pollen of *E. hirsutum*, was somewhat more successful, though plants were obtained only with difficulty. After many failures 11 plants were brought to blossom; and, after six years, 3 more.

Although the plants of the F_1 generation were uniformly partly fertile, showing about 26 per cent. of viable pollen, the plants of the second backcross generation were variable. Four were completely sterile; 8 were partly fertile, the per cent. of viable pollen running from 21 to 71. Five of these plants were very similar to *E. hirsutum*. Four were fertile. One was sterile.

In the third backcross generation, the few progeny obtained from the sterile (male) plants were again sterile, while the plants obtained from the partly fertile mothers exhibited a variable amount of fertility, though less than that shown by the mother plants.

In the fourth backcrossed generation, the fertility again was reduced. More than half of the plants were completely sterile. Nevertheless, it is to be noted that the fertility of some of the fertile plants was between 80 and 100 per cent.

The fifth backcrossed generation segregated into sterile, partially fertile and fertile plants in a manner precisely similar to the fourth generation.

The results from the fourth to the seventh backcrossed generations are comparable. Michaelis then assumed that the chromosomal outfit of the plants was identical with that of *E. hirsutum*, though the plasma was still the plasma of *E. luteum*. Reciprocal crosses were therefore made in the belief that this procedure would determine

whether an influence of a true plasmon was shown. He did find a difference in the reciprocal crosses, reduced fertility being found only in the *E. luteum* plasma. Of 2,461 plants in *E. hirsutum* plasma, only 14 were sterile.

My feeling, after a careful examination of the results of Michaelis, is that, although they lead to no definite decision, they tend to be more easily explained by nuclear action than by plasmon action. I would not deny plasmon action in the sense of Correns, but I would question plasmon action in the sense of Von Wettstein. One can not avoid the conclusion that a large amount of segregation was exhibited and that this segregation was probably accompanied by differential pollen-tube growth. At all events the later backcrossed generations were the result of segregation and selection. And it is not at all certain that the genoms of the backcrossed hybrids even approached identity with *E. hirsutum*. When, in the seventh backcrossed generation, the reciprocal crosses B. C. gen. 7 $\times$ *E. hirsutum* and *E. hirsutum* $\times$ B. C. gen. 7 were made, therefore, various possibilities were to be expected, any one of which might explain the results obtained. There may, of course, be an influence of a Von Wettstein plasmon. But it is just as likely, owing to the persistence of extraordinary viable chromosomal combinations in the gametes of the female but not in the male —this distinction being known to be common—that nuclear combinations were possible where the backcrossed hybrid was the female which were impossible when *E. hirsutum* was the female. For similar reasons it is possible that the reciprocal differences found were due to a plasmon effect of the type postulated by Correns. Again, it is possible that differential pollen-tube growth intervened to influence the results in the mating where the backcrossed haploid was the female.

It is no easier to fix upon critical evidence in the work of Sirks (1932) on Vicia. Besides the direct influence of seed size, which is so commonly observed, Sirks found that plasma influence is exhibited in three ways and is

correlated with the systematic position of the two parents. The species is divided into several subspecies, of which the *major* and the *minor* group are the most important. Reciprocal crosses within each group are alike; reciprocal crosses between the groups show marked differences.

In the course of his experiments, Sirks found that the development of certain organs is conditioned by the same basic factor supplemented by the action of different modifying factors within the group. If, now, crosses are made between groups having genes whose behavior is known when crosses are made within the group, differences are observed. Stem growth is better in *minor* plasma than it is in *major* plasma, though there is no difference in leaf development. Fruit development, on the other hand, is better in *major* plasma. In general, Sirks feels that the two plasmas have different reactions on a given genotype. His conclusion is plausible, of course; but one is inclined to offer the criticism that while the presence of certain genes can be ascertained, there is no way of ascertaining the identity of genotype constitutions as wholes.

The second way in which the two plasmas differ is in the rejection of certain gene combinations. One entire linkage group was found to be viable in the homozygous condition in the *major* plasma, but was lethal in the *minor* plasma. Sirks interpreted these results by assuming a diffused gene. Stern (1932), however, believes that the non-appearance of this linkage group is not due to a diffused gene, but rather to absence of crossovers. A similar phenomenon is known in maize-teosinte crosses.

The third way in which segregation depends upon the type of cytoplasm concerned is found in a variegation dependent upon a pair of allelomorphs V and v. In *typica* plasm, the segregation is regularly 1VV : 2Vv : 1vv. In *variegata* plasm, those gametes in one of the sexes that carry the v factor are eliminated, giving the results ordinarily to be expected by a backcross VV $\times$ Vv. In

the *subtypica* plasm, the dominant V gene is eliminated in one of the sexes, thus bringing about a typical segregation of the type to be expected in the cross Vv × vv.

It is readily seen that in the Vicia experiments there is no proof of a plasmon of the Von Wettstein type. The best evidence in favor of the existence of such a system comes from the experiments of Von Wettstein himself on mosses.

These experiments (Von Wettstein, 1924, 1926, 1928) are comprehensive and have been carried out with great ingenuity. The family used was the Funariaceae, where there is an extraordinary compatibility between genera, and where there is an easy means of recognizing segregates through observations on the gametophytes. The material possesses a further advantage in that polyploid gametophytes varying from 2n to 8n can be produced by regeneration. But it has a disadvantage in that cytological investigations are very difficult. Von Wettstein has been able to determine that the diploid chromosome number in *Funaria hygrometrica* is 14 (there are also tetraploid and octoploid forms), and in Physcomitrella is ca. 16; but he has not been able to study chromosome behavior.

Von Wettstein's crosses may be divided into four types. Type I includes varietal crosses within the species *Funaria hygrometrica.* Here there is no difference between reciprocals, and the numerous allelomorphic pairs of genes segregate and recombine in the ordinary manner.

Type II consists of crosses between two species of the genus Funaria, *F. hygrometrica* and *F. mediterranea.* Here the reciprocal crosses were found to be very different. Segregation occurred, and new combinations were found in the F_2 gametophytes; but in many characteristics the type of the paternal species was not recovered. There was a shift of the phenotype toward the mother. Nevertheless, a considerable amount of variation was observed. In some organs, such as the multi-

cellular hairs (paraphyses) lying between the sexual organs, genic constitution appeared to control the situation completely, as in Type I; in other organs, such as the leaves, the dominant influence appeared to be the cytoplasm. Similar results were obtained in later generations.

Type III results came from crosses between two genera which are not so very far apart taxonomically. *Funaria hygrometrica* and *Physcomitrium piriforme* are examples of the species used. The reciprocals were, in general, similar, and produced gametophyte segregants. But these segregants were all identical with, or similar to, the mother plants. No plants were found that were similar to the species used as the father. Since this failure to obtain expected recombinations was accompanied by a high percentage of spore sterility, Von Wettstein interprets the results by the assumption that gene combinations approaching those of the paternal species are inviable in the cytoplasm of the maternal species.

Type IV results were obtained when species of the genus Funaria, or other closely related genera, were combined with species of the genus Physcomitrella, which is often placed in a separate subfamily. Here the cross is possible in only one direction, and spore sterility is very high. Only plants similar to the mother species were obtained. In this group, one case was found that the investigator believed had special importance because he could analyze the entire spore tetrad. In each tetrad 2 spores germinated and grew, while 2 spores were inviable. Von Wettstein appears to believe that in this case segregation of whole genoms occur, and only those are viable which are identical with those of the mother species. In other words, the genom of the paternal species will not function in the cytoplasm of the mother.

Now, though Von Wettstein used the above results as the basis of an argument in favor of the existence of an independently constituted plasmon carrying hereditary factors, he recognized that such evidence was not critical.

He therefore undertook to gather more critical evidence. He was aided in this task by favorable circumstances. It is possible, in the mosses, to regenerate gametophytes with diploid, tetraploid and even octoploid genoms from sporophytic tissue without the intervention of spore formation and meiosis. By utilizing this characteristic he was able to combine haploids with haploids, diploids with diploids and tetraploids with tetraploids, and, in addition, to combine forms possessing from one to four genoms of one species with forms having from one to four genoms of a second species. Three kinds of experiments were undertaken, particularly with the combination *Physcomitrium piriforme* (Pi) and *Funaria hygrometrica* (Hy) which belonged to Type IV.

The first experiment was a succession of selections of plants most similar to the type of the father species Hy. They were always sterile.

The second experiment was to combine one Pi genom with one, two or three Hy genoms. Thus the cytoplasm of Pi was under the influence of the activity of various quantities of paternal chromatin. The results for 5 generations were identical. The viable spores always produced plants identical with those of the maternal species.

The third experiment was a succession of backcrosses with haploid genoms of Hy. The resulting plants were always Pi. This was true after 5 generations.

It should also be mentioned that some backcrosses were undertaken in combinations belonging to types II and III. Here, also, the influence of the mother cytoplasm persisted, though the author himself admits that the number of progeny obtained is too small to give a clear picture of the situation.

Discussion and Conclusions

It should be obvious to any one who has followed the crossing experiments of the past decade or so, where genic analyses of a high order of precision have been made, that it is *ordinarily* unnecessary to visualize the

cytoplasm as a vehicle for carrying hereditary factors. The cytoplasm behaves as a neutral agent. The determinants are genic differences. This fact is shown most definitely, perhaps, by repeated observations that reciprocal crosses give identical results, although the cytoplasmic contributions of the male are, in most cases, negligible when compared with those of the female. It follows that there can be no differential cytoplasmic influence proportional to the quantity of substance in action. And one may go still further. Genetic evidence no longer rests on an interpretation of pedigree-culture data made by fitting the observations to the probability curve determined by the free assortment of paired genes. Linkage experiments have shown that the genes are grouped in a specific manner. Moreover, many unusual cases of inheritance have been interpreted satisfactorily simply by assuming unusual distribution of determinative chromatin acting in a neutral cytoplasm. In such situations, the results obtained are those to be expected under chromatin control if there be gene duplications, gene deficiencies or unusual gene groupings; and cytological observations have given definite proof of the validity of the analyses. It is reasonable, therefore, to conclude that in intra-specific crosses, where adult characteristics only are recorded—which are the source from which geneticists have drawn over 99 per cent. of their data—any possible hereditary contributions from the cytoplasm of the two parents are virtually identical.

These facts alone would render improbable the idea, recently put forward by Castle (1933), that cytoplasmic differences in the parents furnish the basis for the transmission of quantitative characters, even if one could justify the neglect of the really large amount of data from reciprocal crosses and the not insignificant amount of data from linkage experiments where there is positive evidence against it.

Where juvenile characteristics are studied, the situation appears to be somewhat different, although this dif-

ference proves to be essentially superficial. Here the influence of the mother often dominates, and this influence is presumably due to the preponderant amount of maternal cytoplasm present. If this interpretation is correct—and one can hardly evade it—it follows that occasionally the cytoplasms of individuals from races nearly enough related to produce fertile hybrids, may be sufficiently differentiated to be effective in producing diversity in reciprocal crosses. This is a highly important fact, but it is not a fact which makes it necessary to assume the existence of cytoplasmic units of heredity. The maternal cytoplasm has been laid down under the influence of the maternal nucleus; and this nucleus is made up of biparental contributions of chromatin. It thus becomes possible to follow the influence of chromosome distribution on the characteristics in question. When this is done, it is found that the determinative influence of the nucleus is just as much in evidence here as in other characteristics. Action is simply delayed. One may think of the situation as one in which gene action of the maternal generation holds a certain executive power after the filial generation has begun. It is a situation not without its analogies in the environmental influence exerted by the mother in the mammals and the seed plants. It must not be forgotten, however, that this control is fleeting. The activity of the filial genes has been shown to begin at very early stages of ontogeny.

Thus far, then, the evidence leads to the belief that, though the cytoplasm and the nucleus cooperate in *development,* the only ascertained agent of *heredity* is the nucleus. The data of embryology lead to the same point of view. Cytoplasmic differentiation occurs; and this differentiation is an important part of the machinery of developmental physiology. But there is not a single embryological fact incompatible with the idea of complete nuclear control; although, in the earlier cleavage stages, this control may be maternal. There are simply no data available that enable us to decide whether there is an

effective plasmon independent of the nucleus or not. What we do have to go on with is this: If a plasmon exists, it is neutral to the determinative powers of the genes in ordinary crosses and must be virtually identical in the parents of nearly all hybridizable types.

If the evidence necessary for a critical decision is to be obtained, therefore, it must come from a study of merogony or of the occasional reciprocal crosses which are different.

No acceptable instances of merogony are known in animals. There are seven in plants. In six, there is no evidence of cytoplasmic influence. The nuclei appear to be the sole arbiters of destiny. The one case where it is claimed that there is a noticeable influence of the plasma is that of Harder on the Basidiomycetes Schizophyllum and Pholiota. Here it is proper, I believe, to withhold judgment. The influence which Harder thought he found is of a very hazy and tenuous kind, with one exception; it is the type of change where there is poor development, and is probably comparable to the variations produced by environmental factors. The one definite character noted was sex, and sex was controlled by the nucleus.

It would be very much worth while if a large number of instances of merogony could be collected. If no influence of the plasma were detectable, it would lead biologists to a decision against the plasmon idea, though the criticism that it was negative evidence would stand. But if plasmatic influence were found, there would still be no evidence of a plasmon, since this influence could be ascribed to disharmony between a plasma produced in the presence of the maternal nucleus and the unrelated paternal nucleus. Critical evidence in favor of the plasmon hypothesis could come only if the plasma of species A continued to show an influence on the characteristics of the organism during successive generations of influence of the nuclei of species B. There are two such examples, the Euchlaena case and the Vicia case. No significant plasmatic influence was found in either one.

From the evidence on reciprocal crosses, one should reject that on the *albomaculata* variegation, since the most plausible explanation is diseased cytoplasm, and since voluminous observations have been made proving that plastid differences are ordinarily controlled by nuclear activity. There remains the work on gyno-dioecious plants, on male steriles, on Epilobium, and on the mosses. Is it acceptable proof of a plasmon?

The investigations of Correns on the two gyno-dioecious species Satureia and Cirsium are, in one sense, the most satisfactory of the group, since here there is the smallest number of extraneous variables. Hermaphrodites selfed continue to give only hermaphrodites, while females by hermaphrodites continue to give only females, without much visible elimination of gametes or zygotes. Under simple assumptions of gene recombinations this is impossible, for the genom of the female would ultimately be replaced by the genom of the hermaphrodite. It would be possible, under gene control, to require the replacement of any given number of genes X before the female became a hermaphrodite. The time necessary for the change, therefore, might be extended more or less indefinitely; but when the shift was once made, femaleness would have been eliminated for all time. There are other ways, under gene control, to retain the original situation as regards the sexes; but all such schemes require peculiar types of balanced lethals and hence high degrees of sterility. This is not in accordance with the facts.

But there is a possible explanation of these results which has not yet been eliminated. This is selective pollen-tube growth, with or without selective elimination of female gametes. The simplest form of this hypothesis is to assume that the hermaphrodite is aa and the female Aa, and further that the *a* gametes of the female are not viable or are not fertilized. This serves to continue the two types aa and Aa. If it be asked why the *a* gametes of the female are not functional when those of the hermaphrodite are functional, one may reply by locating the

effective cause in gene A. Gene A may work through the plasma though not through a plasmon.

One may also locate the determining agent in the hermaphrodite. The female becomes AA, and the hermaphrodite becomes Aa. Only A pollen functions on female plants. Hermaphrodites retain the Aa composition through lethal elimination of homozygotes or through selective fertilization of unlike gametes.

Both these hypotheses are possible and even plausible, and both can be tested. It is not wise to overemphasize the facts reported by Correns, therefore, until the entire cytological picture becomes clear, for one must remember (a) that most gyno-dioecious plants do not behave in the manner discovered for these two species, but instead show typical Mendelian segregation and (b) that these are intra-specific crosses where the action of a possible plasmon is almost always the same for selfs and crosses.

It is less easy to escape the plasmon hypothesis in the case of the male steriles. Rhoades presumably replaced each of the ten chromosomes in his maize experiments, following the results by using chromosome markers in each case; and he was able to discover no chromosome influence. And in maize the cytological facts are well known. It hardly seems possible that a situation such as we have just hypothesized for the gyno-dioecious plants could exist in this case. Yet I do not feel that the possibility has been eliminated entirely. Dr. Rhoades tells me that although three or four generations of backcrosses have given identical results—that is, similar production of male steriles in each generation—he is now beginning to obtain irregularities. And this is exactly what I have found for the male steriles in Nicotiana. Whether the cause of such irregularities lies in selective elimination of a given type of female gamete, in selective pollen-tube growth, or in some kind of nuclear condition not checked by the particular gene markers used in the chromosome substitution experiments, can not be stated at present; but it certainly seems inadvisable to say that the plas-

mon has been definitely proved to be the basis of the phenomenon.

In regard to the Epilobium work, it is my opinion that Lehmann and his students have the better of the argument at the present time. This is not to say that they have proved that no plasmon exists. It is unlikely that Lehmann would make such a claim. He would probably say, and with justice, that the supposed plasmatic effect must be shown to continue unchanged in a succession of backcrosses, that the entire cytological situation must be set forth in a detailed manner in order to see whether selective gametic elimination occurs in either the male or the female, and that the question of selective pollen-tube growth must be investigated carefully. In spite of the immense amount of work already done on the reciprocal crosses between *E. hirsutum* and *E. luteum,* much still remains to be done. One is not hypercritical, it seems to me, if one is suspicious of the fact that other species crosses in Epilobium behave as if their differences are entirely controlled by nuclear activity. It is hardly to be expected that the effects of plasmon activity should be manifested in only one combination out of several in a single genus.

The criticisms of the work on male sterility apply to supposed plasmatic effects in Vicia.

And finally, there are the investigations on mosses. What is to be said of them? Von Wettstein's work is magnificent, his theoretical interpretation of the results is plausible. But, though the interpretation merits respectful and sympathetic consideration, it is not absolutely established. Heitz has shown that certain dioecious mosses have sex chromosomes. The situation in monoecious mosses is still debatable. It ought to be determinable. In fact, it may be noted, in passing, that we know little about what determines conditions in any monoecious plants, or what causes the production of male gametes and of female gametes in hermaphrodites. Again, we are ignorant of whether or not selective fer-

tilization can take place. The male gametes float down the canal and presumably are presented to the eggs for acceptance without favor; but there may be blocks to fertilization by certain gametes comparable to those found in the Ascidian, *Ciona intestinalis*.

The four types of crosses made by Von Wettstein and the backcrossing experiments are all compatible with the idea of a plasmon. They are not, however, of equal weight as critical proof of its existence. In Type I, intraspecific crosses, any assumed plasmon contribution must be identical in the species involved. In Type II, intrageneric crosses, there are facts which are most simply interpreted as plasmon action, particularly those obtained from the backcrosses; but in the absence of knowledge of the cytological details, the lack of information as to selective fertilization, and the effect of replacing marked chromosomes, it can not be said to be conclusive. In Type III, crosses between nearly related genera, where segregants like the father were not obtained, there is evidence tending to show plasmatic incompatibility with paternal genoms, but no pertinent evidence that the plasmon is a carrier of hereditary factors. The last remark holds also for crosses between unrelated genera, which are grouped together as Type IV.

The backcrossing experiments made with the Type III crosses are also very suggestive; but not, I venture to say, wholly conclusive. They establish the fact that there is a marked effect on development when cytoplasm from certain genera meets genoms from other genera. The two do not fit, and developmental processes show this lack of compatibility. This is true, no matter whether the genoms contributed by the two parents are 1:1, 1:2, or 1:3. I am unable to see, however, that these facts are either for or against the existence of a plasmon. Such evidence is more likely to be obtained from backcrosses in Type II, where normal segregation appears to obtain. This evidence at present is fragmentary.

The plasma, then, is an active part of the machinery in

development. Ordinarily it is neutral, and may be neglected in comparing the effects of the genes. In other words, if there are plasmatic hereditary factors, they are identical in virtually all the types of crosses commonly studied and can not produce distinctive effects. There are, on the other hand, a small number of crosses, usually between less closely related organisms, where the plasma from one parent shows disharmony with the genom from the second parent. A marked difference in reciprocal crosses is found. The facts from the study of such crosses are highly suggestive of a true plasmon; but, for the reasons pointed out, they can not be said, as yet, to have established its existence beyond cavil. Moreover, there is additional cause for agnosticism in the data from cases of merogony, where definite plasmatic effects are lacking. Weighing all the evidence for and against the plasmon, therefore, one is forced to the Scotch verdict "not proven." But to-morrow or the next day this verdict may be incorrect.

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CHROMOSOMES INVOLVED IN A SERIES OF INTERCHANGES IN MAIZE

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DURING 1931, a number of new semisterile lines of maize were tested. One of these (culture 6452) was obtained from seed x-rayed at Pasadena. The balance (cultures 6460 to 6477) were from Dr. L. J. Stadler's cultures obtained by x-ray treatment at Columbia, Missouri. The general form of test used was to cross with previously known interchanges and to examine sporocytes of the F_1 plants for chromosome configurations at diakinesis.

These tests were undertaken to obtain chromosomal interchanges for further study and to isolate a series of tester stocks for use in identifying chromosomes in a larger series of interchanges now under investigation.

CHROMOSOME CONSTITUTION OF INTERCHANGES USED AS TESTERS

In designating the chromosomes of maize, the following nomenclature will be used. The chromosomes are listed from longest to shortest.

Chromosome	Linkage Group
1	*P br f* bm_2
2	*lg b* v_4
3	*a na* ts_4
4	*su Tu* gl_3
5	v_2 *pr* bm_1
6	*y pl sm*
7	gl_1 *ra ij*
8	*j*
9	*c sh wx*
10	*r g*

Six known interchanges were used as testers. These are listed below with the symbols used for designating the interchange gamete of each.

Semisterile–1, involving chromosomes 1 (*P br f* bm_2) and 2 (*lg b* v_4). Brink 1927, Brink and Burnham 1929, Brink and Cooper 1931. T 1 · 2

Semisterile–2, involving chromosomes 8 (*j*) and 9 (*c sh wx*). Burnham 1930, McClintock 1930. T 8 · 9

Semisterile–3, involving chromosomes 1 (*P br f* bm_2) and 7 (gl_4 *ra ij*). Burnham 1930. T 1 · 7

Semisterile–5, involving chromosomes 1 (*P br f* bm_2) and 6 (*y Pl sm*). Cooper and Brink 1931. T 1 · 6

Semisterile–6, involving chromosomes 5 (v_2 *pr* bm_1) and 7 (gl_1 *ra ij*). Burnham unpublished. T 5 · 7

Semisterile–7, involving chromosomes 2 (*lg b* v_4) and 3 (*a na* ts_4). Burnham unpublished. T 2 · 3

Procedure

Each of the new interchanges was crossed with the interchange testers listed above. Sporocytes of the F_1 plants were examined at diakinesis. Where the new interchange involves neither of the two chromosomes interchanged in the tester, two separate rings (or chains) of four chromosomes each are formed. Where the new interchange involves one of the two chromosomes interchanged in the tester, a ring of six is formed instead. Chromosome 6 is easily recognized by its attachment to the nucleolus. Chromosome 10 is smaller than the others and is usually recognizable especially in crosses with semisterile–2 where chromosomes 8 and 9 are in a ring.

Data

The results of sporocyte examinations are summarized in Table 1. Two rings or chains of four chromosomes each are indicated by "4 + 4." Similarly, "6" indicates a ring of six chromosomes. The remaining chromosomes are present as pairs (bivalents). The second column was obtained from crosses with a stock homozygous (X-normal) for both interchanges (Xn–1, Xn–2). In the column marked "satellite," a plus sign indicates that the satellite chromosome (No. 6) is included in the ring. This is shown by the attachment of the ring to the nucleolus. Under "No. 10" a plus sign indicates that chromosome 10 is included in the ring. This was mostly determined

TABLE 1

CHROMOSOME CONFIGURATIONS IN CROSSES OF NEW SEMISTERILES WITH KNOWN INTERCHANGES

Culture	Tester							Satellite	No. 10	Identified by linkage	Identified cytologically
	T1·2	T1·2 T8·9	T8·9	T1·7	T1·6	T5·7	T2·3				
6452			4+4	4+4			4+4	+	–	5, 6	5, 6
6460	6		6	4+4		4+4	6	–	–	2, 9	2, 9
6462	4+4	4+4+4		4+4	4+4	6	4+4	–	–	5	
6465		6+4	6	4+4	4+4		6	–	–	3, 9	3, 9
6466	6	6+4	4+4	6				–	+	1, 10	1, 10
6467	4+4	6+4	6	4+4	4+4	4+4	4+4	–	–	4, 8	4, 8
6468	4+4		4+4	4+4		6	6	–	–	5	
6470	4+4		6	4+4	6	4+4		+	–	6, 9	6, 9
6471	6		4+4	4+4			6	+	–	2, 6	2, 6
6472	4+4	4+4+4	4+4	4+4	4+4		4+4	–	–	4, 5	
6473	6		4+4	4+4		4+4	6	–	+	2, 10	2, 10
6474	4+4		4+4	6	4+4	6	6	–	–	7	3, 7
6475	4+4		4+4	6	4+4		4+4	–	–	5, 7	5, 7
6477	4+4	6+4		4+4	4+4		6	–	–	3	3, 8

by examination of the free chromosomes in crosses involving semisterile–2.

There were no interchanges available involving chromosome 4, so it was first determined by elimination in cultures 6462, 6467 and 6472. This determination has since been confirmed by linkage tests with sugary and by examination of pachytene figures.

Chromosomes 8 and 9 could not be distinguished from the intercross data, so were determined by prophase examination and later checked by linkage and by intercrosses between the new semisteriles.

Most of the chromosome determinations have been confirmed by linkage tests and by a study of pachytene figures. These confirmations are listed in the last two columns of Table 1. Only two of the interchanges lack both of these confirmations, but they are clearly established by the intercross data. These are 6462, which must be 4 · 5 by elimination, and 6468, which involves chromosome 3 as shown by the intercrosses with T 1 · 2 and T 2 · 3.

Some intercrosses were made between the different new interchanges. Data on these are given in Table 2. In all cases the results are in agreement with the interpretations given in Table 1.

Each one of these interchanges is being studied both genetically and cytologically. The results of these studies will be published later.

The writers wish to acknowledge their indebtedness to Dr. L. J. Stadler for the seed from his x-rayed lines; to Dr. C. R. Burnham for permission to utilize his unpublished interchanges as testers, and to Miss Gertrude Geertsen, laboratory technician, who has prepared most of the slides.

Summary

Fourteen chromosomal interchanges were isolated from x-rayed maize. Intercrosses with known interchanges, linkage and cytological identification were used

TABLE 2

CHROMOSOME CONFIGURATIONS IN INTERCROSSES OF NEW SEMISTERILES

Intercross	Chromosomes involved	Chromosome configuration
6452 × 6462	5, 6 + 4, 5	6
6452 × 6465	5, 6 + 3, 9	4 + 4
6452 × 6468	5, 6 + 3, 5	6
6452 × 6472	5, 6 + 4, 5	6
6460 × 6462	2, 9 + 4, 5	4 + 4
6460 × 6465	2, 9 + 3, 9	6
6460 × 6467	2, 9 + 4, 8	4 + 4
6460 × 6472	2, 9 + 4, 5	4 + 4
6462 × 6468	4, 5 + 3, 5	6
6462 × 6471	4, 5 + 2, 6	4 + 4
6462 × 6473	4, 5 + 2, 10	4 + 4
6462 × 6474	4, 5 + 3, 7	4 + 4
6465 × 6470	3, 9 + 6, 9	6
6465 × 6472	3, 9 + 4, 5	4 + 4
6465 × 6477	3, 9 + 3, 8	6
6466 × 6470	1, 10 + 6, 9	4 + 4
6466 × 6473	1, 10 + 2, 10	6
6467 × 6470	4, 8 + 6, 9	4 + 4
6467 × 6472	4, 8 + 4, 5	6
6467 × 6475	4, 8 + 5, 7	4 + 4
6467 × 6477	4, 8 + 3, 8	6
6468 × 6470	3, 5 + 6, 9	4 + 4
6468 × 6471	3, 5 + 2, 6	4 + 4
6468 × 6472	3, 5 + 4, 5	6
6468 × 6475	3, 5 + 5, 7	6
6468 × 6477	3, 5 + 3, 8	6
6471 × 6472	2, 6 + 4, 5	4 + 4
6472 × 6575	4, 5 + 5, 7	6

to determine the chromosomes involved in these interchanges.

The chromosomes interchanged are as follows:

6452	5 . 6
6460	2 . 9
6462	4 . 5
6465	3 . 9
6466	1 . 10
6467	4 . 8
6468	3 . 5
6470	6 . 9
6471	2 . 6
6472	4 . 5
6473	2 . 10
6474	3 . 7
6475	5 . 7
6477	3 . 8

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CHROMOSOME NUMBERS IN XIPHOPHORIN FISHES

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INTRODUCTION

GENETICALLY, Platypoecilus exhibits the WZ type of sex-linked inheritance (Bellamy 1928, Gordon 1927, Fraser and Gordon 1929), while Lebistes shows the XY type (Winge 1922). *Xiphophorus hellerii,* which is closely related to Platypoecilus, has been studied genetically by Kosswig (1933) and by Gordon (unpublished), but no evidence of sex linkage has been demonstrated. Friess (1933) was unable to confirm Harm's (1926) tentative conclusion that Xiphophorus had the XY type of sex determination on the basis of the latter's work on sex reversals. Under the present taxonomic arrangement, all the above species are included in the same subfamily, Poeciliinae (Hubbs 1924). The occurrence of such diverse conditions in closely related forms has suggested the desirability of attacking the problem from the cytological standpoint.

In his study of the chromosomes of *Lebistes reticulatus,* Winge (1922) was unable to furnish any cytological evidence for the existence of sex chromosomes in that species. Vaupel (1929) suggested that the existence of a pair of chromosomes which pass to the poles ahead of the others might represent sex chromosomes in Lebistes, but she does not regard the evidence as conclusive. Iriki (1932) fails to find any evidence for sex chromosomes in either Oryzias (Aplocheilus) or Lebistes. Other suggestions as to the cytological identification of sex chromosomes in fish have been made by Geiser (1924), for *Gambusia holbrooki,* and Foley (1926) for *Umbra limi.* In no case has the existence of sex chromosomes in fishes been established cytologically. For additional literature on the chromosomes of fish the reader is referred to the excellent list prepared by Oguma and Makino (1932).

Ralston (1933) has recently published a preliminary note on the chromosomes of some species of Xiphophorus and Platypoecilus. He states that the number of tetrads observed in the first maturation divisions of *P. maculatus* and *P. couchianus* and two species of Xiphophorus is twenty-four. In addition, he suggests that a pair of chromosomes which take their position on the plate before the others, and pass to the poles precociously, represent the sex chromosomes.

The fishes of the genera Platypoecilus and Xiphophorus constitute the tribe Xiphophorini (Hubbs 1924). The fishes of this tribe have a restricted distribution. They are chiefly confined to Mexico. Scattered records indicate that the southern species of Platypoecilus and Xiphophorus reach Honduras and Guatemala.

Hubbs and Gordon in an unpublished manuscript entitled "Fresh-water Fishes of Northeastern Mexico" recognize four species of Platypoecilus and two of Xiphophorus: *P. couchianus* (Girard) from the Rio Grande system, *P. xiphidium* Hubbs and Gordon, MS., from the Rio Sota la Marina system, *P. variatus* Meek and *X. montezumae* Jordan and Snyder from the Rio Panuco system, *P. maculatus* Gunther and *X. hellerii* Heckel from the Rio Papaloapan system and rivers to the south (Fig. 1). The significant fact concerning the distribution is that each species of Platypoecilus is confined to its own drainage system or systems. Correlated with the distinctness of their ranges, the various species may be morphologically differentiated. These statements also apply to the two species of Xiphophorus whose ranges overlap those of the southern species of Platypoecilus. The data on the distribution of the xiphophorin fishes, also, suggested the desirability of a chromosomal study of every species in the tribe as a possible means of ascertaining the origin of these geographical species.

This investigation was aided by a grant from the National Research Council. The material upon which this paper is based was obtained from the laboratory devoted

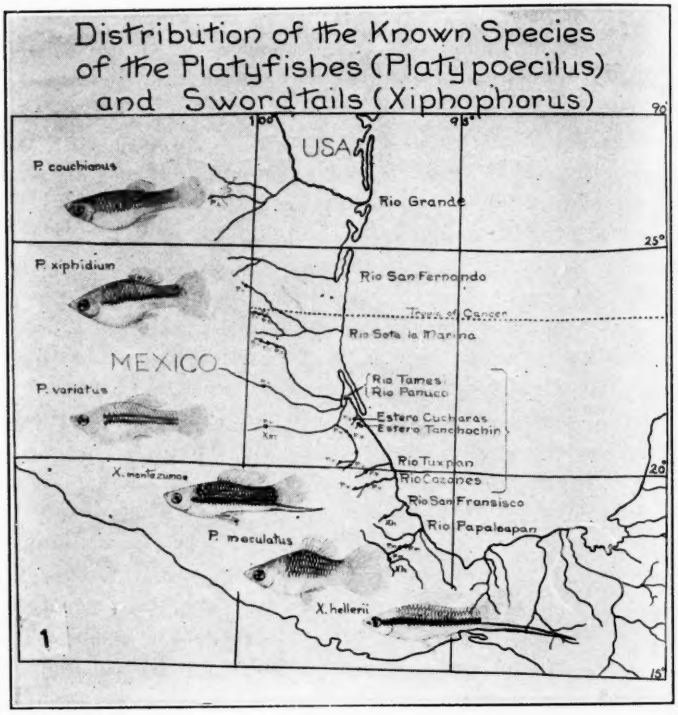


FIG. 1

to the study of the genetic factors in the development of neoplastic growths in hybrid fishes. This is supported by the Heckscher Research Foundation, established by August Heckscher at Cornell University, Ithaca, N. Y.

The authors wish to express their gratitude to Professor H. D. Reed for his suggestions during the course of the study, and to Professor L. W. Sharp for a critical reading of the manuscript.

MATERIALS AND METHODS

The fish employed in the study were either collected in Mexico or bred in the laboratory for genetical purposes from fish originally collected in Mexico in 1930 and 1932. The number of fish of each species studied is:

4 *P. couchianus*, 4 *P. xiphidium*, 4 *P. variatus*, 18 *P. maculatus*, 6 *X. hellerii*, 1 *X. montezumae*. The number of hybrids is: 2 *P. couchianus* × *P. maculatus*, 3 *P. xiphidium* × *P. maculatus*, 3 *P. variatus* × *P. maculatus*, 4 *X. hellerii* × *P. maculatus*.

The testes were removed from decapitated animals, cut into small pieces, and quickly immersed in the fixing fluid. The following fixers gave the best results:

(1) Allen B–15 solution:

75 cc	Saturated aqueous solution, picric acid
25 cc	Commercial formalin
5 cc	Glacial acetic acid

at 37° C. to which 1.5 grams of chromic acid crystals and 2 grams of urea crystals are added just before fixation, and then at 37° C. for two hours.

(2) Nawaschin's modified solution:

15 pts.	1 per cent. chromic acid
4 pts.	Commercial formalin
1 pt.	Glacial acetic acid
1 per cent.	Urea crystals

at 37° C. for initial fixation and then at room temperature for 6 hours.

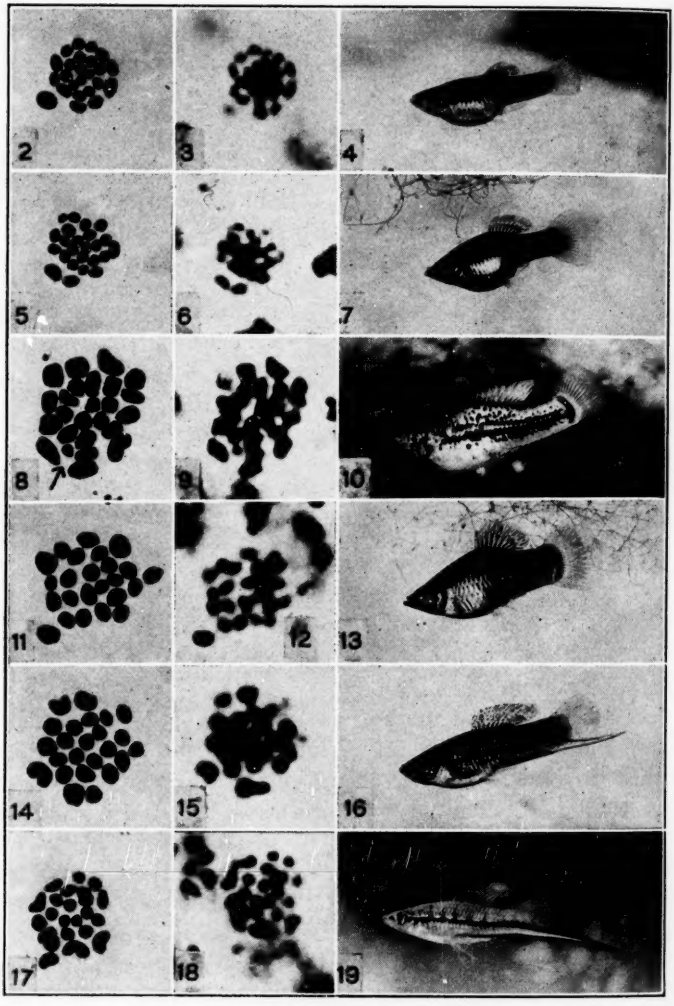
(3) A mixture of 3 parts glacial acetic acid and 7 parts absolute alcohol; fixation period, 24 to 48 hours.

The material fixed in the first two fluids was sectioned and stained with crystal violet. Material fixed in the third fluid was smeared according to the iron-aceto-carmine method. The best results were obtained with material from mature males.

Observations

The chromosomes of the Platypoecilus and Xiphophorus species, as observed at the spermatogonial metaphase, are small, numerous and rod-shaped and show little difference in size. Because of this they are unsuitable for the purpose of making a comparative study of the chromosome morphology of the various species.

The chromosomes at the metaphase of the first meiotic division are small and round, but they may be clearly distinguished and counted. In Figs. 2 to 19 the metaphase



FIGS. 2–19

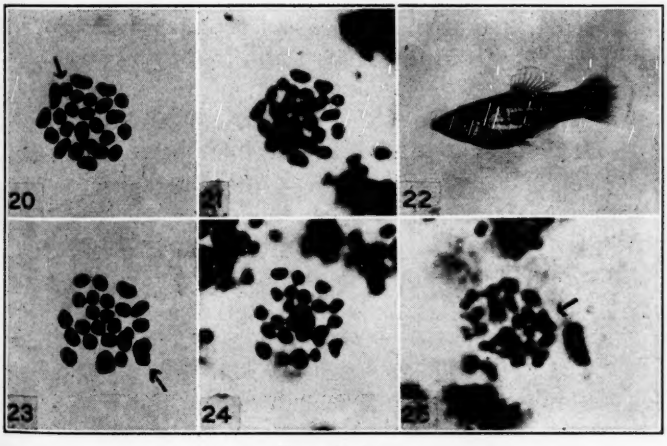
configurations of all the species are illustrated. With the exception of *P. variatus* (Figs. 8, 9, 10) twenty-four tetrads may be recognized in each form. There are a few larger tetrads which usually take a position at the periphery of the plate. The remaining chromosomes are

of approximately the same size. In these chromosome complements one can find very little by which to differentiate one species from another. In the hybrids examined, other than those in which *P. variatus* are involved, complete pairing is found. The hybrids examined were as follows: *P. couchianus* × *P. maculatus*, *P. xiphidium* × *P. maculatus*, *P. variatus* × *P. maculatus* and *X. hellerii* × *P. maculatus*.

In *P. variatus* twenty-five chromosomes were counted at the metaphase of the first maturation division (Figs. 8, 9). One of the chromosomes, indicated by the arrow in Fig. 8, was found to be distinctly smaller than the rest, and evidently univalent. In the hybrid *P. variatus* × *P. maculatus*, some of the cells showed twenty-four chromosomes (Figs. 23, 24) and some twenty-five (Figs. 20, 21). In the twenty-five chromosome cells the smaller chromosome was again observed, while in those with twenty-four evidences of a trivalent were obtained (indicated by the arrows in Figs. 23, 25).

Discussion

In the preliminary account of Ralston (1933) there is no conclusive cytological evidence for the existence of



Figs. 20–25

sex chromosomes in Platypoecilus or Xiphophorus. The existence of a heteropyknotic pair of chromosomes which precede the others to the poles at the first maturation metaphase, even if demonstrated as a constant occurrence, is insufficient evidence upon which to base any conclusion regarding the sex chromosomes. Both sexes must be studied before a cytological basis for heterogamety may be established. During the present series of observations no constantly occurring pair of heteropyknotic chromosomes could be identified. Females, however, were not investigated, and it is possible that a careful study of the oocyte divisions might yield pertinent evidence.

P. variatus was found to be distinct from the other species in showing a small extra univalent chromosome at the metaphase of the first maturation division. When *P. variatus* is crossed with *P. maculatus* this extra chromosome may, together with another chromosome, pair with one of the *maculatus* chromosomes to give a trivalent, or it may remain unpaired as a univalent. Seiler (1925), Kawaguchi (1928) and Sveschnikova (1929) have made similar observations on pairing of chromosomes in intraspecific and interspecific hybrids, and attribute the difference between races or species to the supposed fact that a chromosome of one species corresponds to two formed by fragmentation in the other. It is possible that a similar condition may exist in *P. variatus*.

In all the species of the tribe Xiphophorini, with the exception of *P. variatus*, the lack of distinguishing characters in the chromosomes has made a cytological comparison of the various species impossible up to this time. With respect to *P. variatus*, it would be interesting to examine specimens from the extremities of its range because the specimens studied cytologically represent those taken only in the center of distribution. Local races may reveal intermediate chromosomal conditions.

It was hoped that a determination of the chromosome numbers in each of six species of xiphophorin fishes

might reveal certain clues to the affinities in the tribe. At present the genera Platypoecilus and Xiphophorus are regarded as distinct on the basis of differences in structure of their gonopodia. The individual species within the genera are determined on the basis of the number of dorsal fin rays present and also on the basis of numerical data that represent proportions of the body. The difference in chromosome count in *P. variatus* is not regarded sufficiently significant to suggest that a revision of the xiphophorin fishes should be profitable at present.

The similarity of the xiphophorine chromosomes partly explains the ease with which specific and generic crosses are made in this group, and also, the high degree of fertility that is shown by the first generation hybrids.

Summary

The fishes of the genera Platypoecilus and Xiphophorus constitute the tribe Xiphophorini. The six species of xiphophorin fishes may be regarded as geographical species as they occupy distinctive drainage areas in Mexico.

The chromosome numbers in males of all the species of the tribe Xiphophorini were determined at the first maturation division in males. In *Platypoecilus couchianus, P. xiphidium* and *P. maculatus,* and in *Xiphophorus hellerii* and *X. montezumae* the haploid number of chromosomes is twenty-four. In *P. variatus* the haploid number is twenty-five, the additional univalent chromosome appearing smaller than the bivalents. The chromosomes of F_1 hybrids between *P. variatus* and *P. maculatus* are described. The extra chromosome may, together with another *variatus* chromosome, associate with a *maculatus* chromosome to give a trivalent, or it may remain unpaired as a univalent.

The chromosomes of these species are small and the complements they form are quite similar in appearance. Therefore no cytological characters were found that distinguish the various species of the tribe Xiphophorini, except *P. variatus.*

The similarity of the xiphophorin chromosomes partly explains the ease with which specific and generic crosses are made in this group, and also, the high degree of fertility that is shown by the first generation hybrids.

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EXPLANATION OF FIGURES

The photomicrographs were taken with a Makam camera, Zeiss 1.5 mm obj., Periplan ocular 12x, and somewhat enlarged for reproduction. The drawings were made with the aid of the microscope directly on photomicrographs, which were then bleached with Farmer's reducer. The photographs of living fishes are about four fifths natural size. Fixation Figs. 3, 6, 15, 18, Nawaschin's solution; Figs. 12, 21, 24, Allen B–15 solution; Figs. 9, 25, iron-aceto-carmine smears.

FIG. 1. Distribution of the known species of the Xiphophorini.

FIGS. 2, 3, 4. *P. couchianus* with first maturation metaphase, n = 24. Ser. 2, Sl. 3.

FIGS. 5, 6, 7. *P. xiphidium* with first maturation metaphase, n = 24. Ser. 1, Sl. 7.

FIGS. 8, 9, 10. *P. variatus* with first maturation metaphase, n = 25. Arrow indicates extra chromosome.

FIGS. 11, 12, 13. *P. maculatus* with first maturation metaphase, n = 24. Ser. 2, Sl. 2.

FIGS. 14, 15, 16. *X. montezumae* with first maturation metaphase, n = 24. Ser. 1, Sl. 2.

FIGS. 17, 18, 19. *X. hellerii* with first maturation metaphase, n = 24. Ser. 2, Sl. 6.

FIGS. 20, 21, 22. *P. maculatus* × *P. variatus* with first maturation metaphase showing unpaired chromosome indicated by arrow. Ser. 3, Sl. 3.

FIGS. 23, 24, 25. First maturation metaphases, *P. maculatus* × *P. variatus*. Arrows indicate trivalent. Fig. 24, Ser. 3, Sl. 1.

ON THE REVIVIFICATION OF CERTAIN SPECIES OF PROTOZOA AFTER TWENTY YEARS OF ENCYSTMENT

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DEPARTMENT OF ZOOLOGY, NEW JERSEY COLLEGE FOR WOMEN, RUTGERS UNIVERSITY

IN February of 1914 the writer collected a water sample, together with some bottom deposit, from an old wooden watering trough near Ithaca, N. Y. The sample, of some 200 cc or so in volume, gradually dried up in the same wide-mouthed bottle in which it had been collected in the field. Before it had dried, however, it had been examined, and among others, the following forms of Protozoa had been found to be abundant: *Amoebae guttula* and *limax, Mastigamoeba sp.,* several different forms of minute Mastigophora not further identified, *Chilodon cucullulus, Holophrya sp., Oxytricha bifaria* and a *Colpoda sp.*

After the bottle with its dried sediment had stood around for about a week or so, a slip of paper,[1] bearing the list of species given just above, together with some of the dried sediment, was put into a glass tube 11 mm in diameter and 123 mm long, and the tube sealed at both ends in a Bunsen flame. The ends of the tube were sealed and cooled alternately, the contained material being shaken down into the cooled end and kept cool, while the opposite end was sealed.

The writer's idea at the time (as nearly as he can remember it) was to keep this tube "for a while" and then later to culture its contents to see if any of the formerly active Protozoa would make their reappearance. The tube was kept in a miscellaneous collection of "zoologica," and year after year went by without anything being done to it. At last, twenty years later, in 1934,

[1] This slip bears only the date, "Feb. 1914" and the list of species as given.

it was decided to open the tube and, in the proper medium and with the proper check media and precautions which suggested themselves, to culture the dried sediment and watch the results. Several records of this same general nature have already been published.[2]

On January 17, 1934, 1,000 cc of pond water was filtered through three thicknesses of fine cheese-cloth; to it was added 40 grams of dry chopped hay from an open field; and the mixture boiled one half hour in a 2,000 cc Erlenmeyer flask. Of the resulting light brown infusion, 875 cc was again filtered through three thicknesses of cheese-cloth and then through filter paper, and poured into seven 150 cc Erlenmeyer flasks, 125 to each flask. These flasks were stoppered with absorbent cotton and each one boiled for one hour. One of the flasks (Flask No. I) was then unstoppered and left so during the entire experiment. This was to see if, in a culture so carelessly treated, any Protozoa would later be found. The other flasks were left stoppered and all the flasks set in a quiet corner of the laboratory, in a tray containing a maximum and minimum thermometer, which recorded that during the twenty-five days of the experiment the temperature had fluctuated between 60 and 78 degrees F.

On January 24 the contents of the unstoppered flask (Flask No. I) were shaken up; about 62 cc poured off, centrifuged and the resulting slight sediment examined under the 20 × ocular and 4 mm objective. It contained some few dust particles, such as fragments of wool and cotton fibers and bits of minute angular debris, but no

[2] Dawson, J. A., and Mitchell, W. H., "The Viability of Certain Infusorian Cysts," AM. NAT., 63: 476, September–October, 1929. These investigators came to the conclusion ". . . that cysts of *Oxytricha sp.*, *Spathidium spathula* and *Colpoda cucullus* can remain viable in the dry condition for at least four years, and that cysts of *Podophrya fixa* may live in the same condition for at least nine months." In this same paper the contributions of five other workers on protozoan cyst viability were briefly summarized. The present writer has not examined these latter records, and hence the first six entries in the bibliography at the end of this paper are transcribed as they stand from Dawson's and Mitchell's paper.

trace of protozoan life was found. A slight cloudiness of the liquid and a faint bad odor suggested the presence of bacteria.

In centrifuging this and all other samples, the pipettes and centrifuge tubes were rinsed in boiling water and cooled to room temperature before being used, and kept in covered "hospital jars" when not in use.

On the same day the contents of a stoppered flask (Flask No. II) was given the same treatment. The medium was slightly cloudy, but no odor except that of the hay-infusion character was perceptible. No protozoan life was found in the very slight sediment resulting from centrifuging about 62 cc. The flask was restoppered.

On January 26, 62 cc of the contents of Flask No. III was centrifuged and examined.[3] No Protozoa were present. Flask restoppered.

On this same day, to determine whether the medium that had been prepared was a suitable one for the growth of Protozoa, the remaining contents of Flask No. III were inoculated with a 25 cc sample (the result of centrifuging 100 cc of a pond-water culture) containing the following forms in large numbers: various minute Mastigophora, two larger forms of the same identified as *Chilomonas sp.*, and *Chlamydomonas pulvisculus* (with a brilliant greenish-brown chromatophore), *Amoeba proteus, limax* and *guttula, Arcella vulgaris, Halteria grandinella* (the predominant form—the culture was full of them), *Vorticella sp., Glaucoma scintillans, Bursaria truncatella, Lionotus sp., Holophrya sp.* and *Onychodromus grandis.*

On January 30 one half of the contents of this Flask No. III were centrifuged and examined. The medium had proved a suitable one for Protozoa, for they were all

[3] "Examining" meant that of the centrifuged sediment ten slides were searched on the mechanical stage, under the 20× ocular and 4 mm objective. Each slide contained one drop (about a "minim" of material) under a cover glass. The mechanical stage so moved the slide about that virtually the whole area of the drop under the cover was gone over.

flourishing except that *Amoeba proteus* and *limax* were scarce; *Bursaria truncatella* were few; the *Holophrya* and *Chlamydomonas* had increased and a *Stylonychia* (identified as *mytilis*) had appeared.

On February 2 one half of the remaining contents of this same Flask No. III were centrifuged and examined. *Amoeba proteus* had increased, and the culture was full of them. *Nuclearia simplex* had appeared abundantly (not one had been found on January 30; they appeared like magic!). The minute Mastigophora were not quite so numerous. The other forms were ciliates mentioned before, with the addition of a *Prorodon sp.*, and a large *Frontonia*. *Halteria grandinella* was still the predominant form.

Since the medium had proved a suitable one for Protozoa, on this day it was decided to inoculate it (in one of the stoppered flasks) with the twenty-year-old sediment. Before doing this, another stoppered flask (Flask No. IV) was unstoppered. The medium was cloudy and ill-smelling. One half the contents of this flask was centrifuged and examined under the 20× ocular and 4 mm objective. Many very minute, rod-shaped bacteria were present. No trace of protozoan life was found.

Thirty cc of Flask No. V were poured off and the flask instantly restoppered. An examination of the centrifuged sediment from this flask showed only what was true of Flask No. IV.

Into Flask No. V was shaken the twenty-year-old sediment, and the flask instantly restoppered. It was judged that sufficient evidence had been obtained to show that the medium in general, and that contained especially in Flask No. V, was Protozoa-free. As a future check, another flask, Flask No. VI, had been unstoppered during the time that Flask No. V had remained so. Moreover, 62 cc from Flask No. VI had been centrifuged and examined and had been found to be free from protozoan life.

On February 10 the contents of the inoculated flask

(Flask No. V) was agitated; about 62 cc poured off, centrifuged and examined as before under the 20 × ocular and 4 mm objective. The mixture gave off a distinctly bad odor; was cloudy, and in the ten slides of the centrifuged sediment, many minute Mastigophora were found, and as nearly as could be determined, at least three *Mastigamoeba* sp., per slide! These forms are shown, as drawn from the microscope, in Figs. 1, 2, and 3.

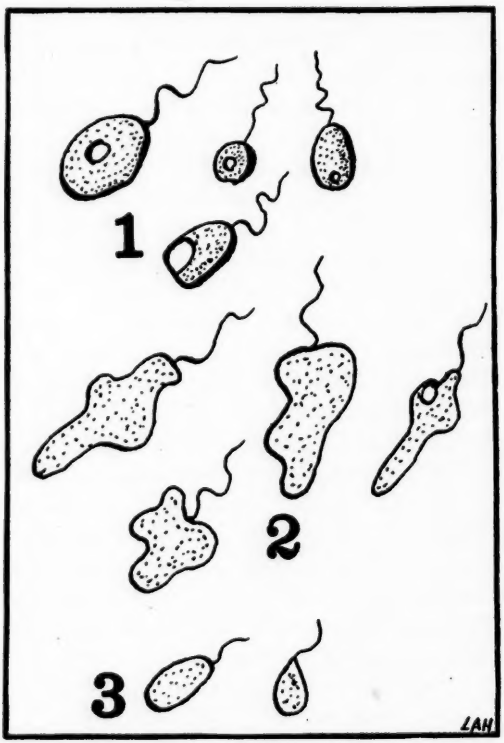

FIG. 1. *Oikomonas sp.*, various individuals, ranging from six to twelve microns, from Flask No. V.

FIG. 2. *Mastigamoeba sp.*, drawn to the same scale. Various individuals from Flask No. V.

FIG. 3. Minute *Mastigophora* from Flask No. I drawn to the same scale.

The Mastigophora were referred to the genus Oikomonas, as given by Conn (1905).

Flask No. VI, which had remained unstoppered only while Flask No. V was being inoculated, was now shaken up and its contents centrifuged and examined. No trace of protozoan life was found.

Flask No. VII was similarly treated, with the same result. This flask had not been unstoppered before. Its contents were quite cloudy and smelled very badly.

Flask No. I (the one which had been left unstoppered from the beginning) was now drained of its remaining contents, and these were centrifuged and examined. In ten slides of this centrifuged sediment examined, many minute Mastigophora were found, similar to the Oikomonas found in Flask No. V, but, it was judged, not of that genus (Fig. 3).

In none of the stoppered, uninoculated flasks did any trace of protozoan life appear.

On February 13 the remainder of the contents of the inoculated Flask No. V was centrifuged and examined. In ten slides examined but three Mastigamoebae were found. The forms called Oikomonas were as numerous as before.

It has seemed to the writer that in view of the precautions taken during this experiment, it is safe to conclude that the two forms which made their appearance in the medium in Flask No. V did so after twenty years of encystment.

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THE GENETICS SOCIETY OF AMERICA

PAPERS READ AT THE BERKELEY MEETING, JUNE 20, 1934

PROFESSOR P. W. WHITING
SECRETARY

1. *Tomato Races with Long and Short A Chromosomes:* MARGARET LESLEY and J. W. LESLEY, University of California, Citrus Experiment Station, Riverside. Among the progeny of triploid tomatoes we have found that some races have long and others short chromosomes associated with the nucleolus at diakinesis in the pollen mother cells. The nucleolar chromosomes of the short type are frequently about half as large as the long chromosomes. From the position of the trivalents in trisomic types it was determined that the A or first chromosomes are associated with the nucleolus. Both long and short A chromosomes have minute "trabants" which extend away from the nucleolus; trabants are not usually found in pollen mother cells. One race with long A chromosomes was outstandingly vegetative until late in the season and one plant of this race was partially male sterile, but two other long chromosome races were quite fertile. *Lycopersicum pimpinellifolium* and F_1 hybrids between it and three wild races of *L. esculentum* all had short A chromosomes. In other words, the nearest wild relatives of the cultivated tomato appear to have short A chromosomes, whereas both long and short-A races have been found in the progeny of three triploids of the cultivated tomato. *L. peruvianum* Dunal resembles the tomato in respects and its pollen applied to tomato stigmas regularly causes the production of seedless fruits. This species has a pair of large A chromosomes associated with the nucleolus at their center. This pair closely resembles the A chromosome pair in our long-A races in size and position. In both the pairs are closely associated at the trabant end and diverge sharply at the opposite end, beginning approximately at the center. Segregation of long and short A races in cultivated tomatoes might result if they were of hybrid origin or if a mutation had occurred under cultivation. Since both long and short-A races may be perfectly fertile both

might continue to exist side by side for a long period. F_1 hybrids between long and short-A races have not yet been studied. Comparison of the size of the chromosomes of trivalents and bivalents in pollen mother cells of trisomic types indicates that the A chromosomes in long-A plants are much the largest and the H chromosomes are among the smallest. Short-A, B, I and J chromosomes are larger than H.

2. *Crossing-over in the X Chromosomes of Attached X Triploid Females of Drosophila melanogaster:* G. W. BEADLE, California Institute of Technology, Pasadena. The experiments reported were undertaken with a view to obtaining genetic information about the method of chromosome conjugation in triploids. XX X females of the constitution ec ct^6 s^2/sc cv v f cr/y^2 bi g^2 B were obtained. Crossing-over was measured in two types of gametes, XX,1A and X,1A. The results show that in all regions except the forked to spindle attachment region, the chromosomes are involved in crossovers at random. In the regions near the spindle attachment, crossing-over between the attached chromosomes is higher than between either one of the attached chromosomes and the free chromosome. The results apparently favor the view that synapsis is by twos and that the attached chromosomes have an advantage in synapsis near the spindle attachment. A second experiment was made in which crossing-over in XX X females of the constitution v f cr/v f B/v cr was studied. Here crossing-over was measured in four types of gametes, X,1A; X,2A; XX,1A; and XX,2A. The results show that crossing-over near the spindle attachment between attached and the free chromosome is low in XX,1A and X,2A gametes and high in XX,2A and X,1A gametes. The additional information obtained in this experiment shows that the results of the first experiment are not to be explained on the basis of the characteristics of synapsis but rather on the basis of an effect of crossing-over near the spindle attachment on correlated orientation of chromosomes on the meiotic *I* equatorial plate. There is no convincing genetic evidence that synapsis is by twos in Drosophila.

3. *The Relation of Adult Body Size to the Rate of Cell Proliferation in the Chicken Embryo:* CECIL T. BLUNN, University

of California, Davis. A comparative study of the effect of racial size on rate of cell proliferation was made in embryos of pure-bred White Leghorn and Rhode Island Red chickens. The mean adult weight of the Rhode Island Reds was approximately twice that of the White Leghorns. Embryos were obtained from eggs incubated in pairs selected with reference to weight and time held in the oviduct. The incubation ages studied were 72 hours, 14 days and 19 days, respectively. Data obtained from a study of the three ages of embryos gave consistent evidence of a differential rate of cell proliferation between the two breeds. At 72 hours and at 14 days the Rhode Island Reds had a larger number of cells and more mitotic figures present in the volumes studied than the White Leghorns. Rhode Island Reds at 19 days had more cells per volume than the White Leghorns, but the difference between the breeds was less than at the earlier ages. The cells of the Rhode Island Red embryos at each age studied were smaller than those of the White Leghorns. The extreme elongation of the individual fibers of the gastrocnemius muscle, studied at 19 days, rendered it unfit for mitotic figure counts. Analysis of the data showed that little, if any, correlation existed between embryo weight and cell number. A study of weights did not reveal differences in embryonic growth rates between the two breeds. A study of cell size, number and mitotic figures, however, divulged the existence of a differential rate of cell proliferation between the two breeds.

4. *Curly, a Recent Mutation in the Rat (Rattus norvegicus):* P. W. GREGORY, University of California, Davis. Curly is apparently a recent mutation in the rat which reduces the number of guard hairs in the coat and causes the guard hairs and vibrissae to be curly in appearance. Curly rats can be classified at birth by the appearance of the vibrissae, which are curly. When the hair of the coat is formed it is somewhat uneven, roughened and curly in appearance. The mode of inheritance and certain linkage relations have been determined.

5. *Coat Color Inheritance in Peromyscus:* R. R. HUESTIS and ELIZABETH BARTO, University of Oregon, Eugene. Data are presented to show that brown and silver coat colors in *Peromyscus* are each due to a pair of recessive genes not allelomorphic

but supplementary in certain effects. Two other presumably recessive coat colors have been discovered; a russet brown with light ears and tail stripe but black underfur and albinism.

6. *Chromosomal Alterations Induced in Plants by X-Radiation:* T. H. GOODSPEED, University of California, Berkeley. Chromosomal alterations induced by high frequency radiation differ in frequency of occurrence rather than in kind from those found in nature. Products and by-products of x-ray treatment of sex cells or vegetative tissues of higher plants are polyploidy and haploidy; polysomy, monosomy, fragment chromosomes and compound chromosomes; chromosomal interchanges (translocation simple and reciprocal), deficiency, deletion, inversion and duplication. These types of induced alteration and their cytogenetic significance can in most cases be illustrated by the results of x-ray treatment of species of *Nicotiana.*

7. *Visible Genes from Aged Seeds:* A. F. BLAKESLEE and A. G. AVERY, Department of Genetics, Carnegie Institution of Washington, Cold Spring Harbor, N. Y. Following the work of Navashin on root tips it has been shown that aging seeds increases both the gene and chromosomal mutations, which bring about pollen abortion in Datura. In the second generation from aged seed, five seed-pan characters, presumably due to "visible" genes, have already appeared in about 350 progenies. More are expected to show when the seedlings are grown to maturity. Since the number of "visible" gene types already obtained from aged seeds is more than that from untreated normal parents throughout all our experience with Datura, it is evident that aging seeds is an effective stimulus to gene mutation.

8. *The Turkey as an Experimental Animal:* V. S. ASMUNDSON, Poultry Division, University of California, Davis. The value of turkeys as experimental animals is shown by comparing them with the domestic fowl. Both species show considerable variation in fecundity, the egg production of turkeys being lower and more nearly what might be expected of birds of these species in their native habitat. In both species there is a marked sex dimorphism in size, in head furnishings and in the plumage color of certain breeds. Sex differences in size are more marked in

turkeys than fowls. It is recognized that differences in the head furnishings of the sexes are largely controlled by hormones. The white tipping on the breast feathers of the Bronze female turkey is also controlled by hormones, since the normally black breast feathers of the male grow in with white tips if the birds are injected with female hormone (oestrin). Most inbreeding experiments with the domesticated fowl have resulted in failure if close inbreeding was used due to the extinction of the inbred line. This difficulty would probably not arise with turkeys since brother-sister matings have been found to give satisfactory results in the hatchability of the eggs, viability of the young to eight weeks of age and in rate of growth. It should, therefore, be possible to build up homogeneous lines of turkeys through inbreeding that would prove useful for genetic and other research.

9. *On the Nature of Chromosome Association in Nicotiana tabacum Haploids:* W. E. LAMMERTS, University of California, Berkeley. Evidence is presented which indicates that a haploid of coral *N. tabacum* shows a higher degree of association at pachytene and 1-M than is found in normal haploids. These associations are mostly non-homologous in nature except for the duplicated coral segment. T-shaped configurations and foldbacks are also found, especially in the coral haploid where the associated sections are much longer. At 1-M a variable number of rod-bivalents are found, the number averaging higher in the coral haploid. The single chiasma may be either terminal, subterminal or interstitial. Fragments are found in both haploids, but their frequency is higher in the coral type, suggesting that crossing-over has occurred in the non-homologously paired regions or in foldbacks. The conclusion is drawn that observation of bivalents at diakinesis and 1-M in haploids and hybrids with variable pairing is not of itself proof of duplicate segments.

10. *The Cytology of a Backcross Population Derived from (Allium cepa × fistulosum) × fistulosum:* S. L. EMSWELLER and H. A. JONES, University of California, Davis. In *Allium fistulosum* the chiasmata of each bivalent at IM are almost entirely localized at the constriction region. In *Allium cepa* they are arranged at random. The hybrid exhibits a random arrangement. Ten of the seventeen backcross plants have localized

chiasmata and seven are random. Pairing frequency of chromosomes at IM in the backcross plants is given and percentage of morphologically good pollen grains compared with these data. Self-fertility of each plant is also determined.

11. *A Consideration of Evolution from a Thermodynamic View-point:* H. F. BLUM, Division of Physiology, University of California Medical School, Berkeley. A certain degree of irreversibility appears necessary for the process of evolution by chance variation and natural selection. This irreversibility may be due in part at least to the functioning of the second law of thermodynamics. It is suggested that both inorganic and organic evolution have taken place under the direction of this irreversible factor, thus accounting in part for the exactness of the fit between organism and environment. The fact that rate of reaction and decrease in free energy are not proportional may account for the variety in both forms of evolution. Photosynthesis should have played an important part in evolution but could not alter its general direction. An attempt is made to build a hypothesis along these lines which will account for certain phases of evolution, particularly orthogenesis.

12. *Glutathione in Relation to Hereditary Size and Growth:* P. W. GREGORY, University of California, Davis. Corrected glutathione values are given for fasted new-born rabbits from races which breed true for small, large and medium adult weight and for various hybrid combinations and backcrosses between these three respective races. The interrelations of genetic constitution for adult size, nutrition, the hypophyseal growth hormone in relation to growth, rate of cell proliferation and the glutathione concentration in the tissues are discussed. In general, the rate of increase in weight, whether regulated by genetic constitution, nutritional conditions or by the hypophyseal growth hormone (in rats) is positively correlated with the glutathione concentration present in the tissues.

13. *Genes in Datura Classified as to Effects on Gametophyte and Sporophyte:* ALBERT F. BLAKESLEE, Department of Genetics, Carnegie Institution of Washington, Cold Spring Harbor, N. Y. The present outline gives a classification of effects presumably

due to individual genes, although a distinction between genes and minor chromosomal abnormalities may be difficult. The genes are listed according to their most conspicuous effects. I. *Genes Affecting the Gametophyte.* (a) Genes affecting chromosomal behavior (studied by A. D. Bergner and Sophia Satina): Three genes when homozygous have the following effects, respectively: (1) Lack of pairing at reduction; (2) doubling of nuclei and formation of giant pollen grains with 2n, 4n and 8n chromosomes; (3) dyad formation with 2n eggs and sperms. (b) Genes affecting pollen grains (studied by J. L. Cartledge): (1) male steriles with no pollen grains: 1 dominant, ♀ fertile; 1 recessive, ♀ fertile; 3 recessives, ♀ sterile. (2) Three recessives when homozygous cause abortion of 85 to 100 per cent. of pollen grains. (3) A gene when homozygous causing the pollen grains to adhere together in strips. (4) Twenty-one cause abortion of pollen grains which contain the gene. (5) Two cause premature germination of pollen grains affected. (c) Genes affecting pollen tube behavior (studied by J. T. Buchholz): (1) Genes preventing germination of individual pollen grains affected. (2) Those causing slow growth of pollen tubes. (3) Those causing bursting of pollen tubes. II. Genes Affecting the Sporophyte (studied by A. G. Avery): These "visible" genes are more familiar to plant breeders and need not be classified in detail. Those causing chlorophyll deficiencies are common. Of these, 20 which die in seed pans are listed as albinos and slightly more which survive are called pales. All told in Datura, about 200 characters in gametophyte and sporophyte have been tentatively classified as due to genes of which about 30 have been located in a particular chromosome.

14. *Reaction of Genes in Feather Follicles:* C. H. DANFORTH, Stanford University, California. Since feather follicles have been found to respond readily to a number of extrinsic factors, the replacement of feathers furnishes a good opportunity for investigating the reactions of genes under varying conditions in adult tissues. The active life of differentiating cells in the growing feather is of short duration, the cells soon becoming cornified in a manner to preserve a permanent record of their brief activity, which is expressed in the form and color of each part of the feather. Further, conditions in the fowl permit one to vary,

separately or in combination, a number of genetic and endocrine factors which influence the output of feather follicles. The endocrine milieu may be changed by several devices, including the injection of extracts and transplantation of skin, and the genetic factors may be varied by appropriate breeding procedures and by the production of such graft-hybrid follicles as sometimes arise from cells derived from both donor and host following skin grafting. Analysis of the interaction of hormones and genes shows that these two classes of factors occasionally show a considerable degree of similarity in their behavior and that sometimes a hormone, like a gene, may be necessary for the realization of a particular trait; but fundamentally the hormones appear to be essentially passive in a biological sense, being features of the internal environment with which certain tissues in some species have developed a capacity to react. In other species, this capacity is not present at all, or the reaction is with different hormones. Tests involving the hormones theelin and thyroxin, and the genes for black, yellow and white in plumage of the fowl indicate that the interrelation of the genes and hormones is in a continual state of flux, even during adult life. Graft mosaics show that cells from the two genotypes contribute in different degrees to the determination of characters in successive feathers from the same follicle. Whether this fact will prove to be of greater significance for genetics or for morphogenesis is still uncertain, but some of the effects seem to be explained best on the assumption of an interaction between genes in different cells. The latter assumption, if correct, may have a bearing on some cases of supposed non-disjunction.

SHORTER ARTICLES AND DISCUSSION

CHROMOSOME FRAGMENTATION IN *LILIUM TIGRINUM* KER.

IRREGULARITIES in the behavior of chromosomes during meiosis have received considerable attention in cytogenetic investigations. Chromosome lagging and fragmentation have been found to be associated with certain types of genetic behavior. Darlington (1932[1]) and Sansome and Philp (1932[2]) have reviewed representative cases and have discussed the genetic interpretations of these phenomena.

An interesting type of fragmentation associated with lagging occurs in *Lilium tigrinum* Ker. A collection of anthers made at Ann Arbor, Michigan, in 1925 exhibited such marked irregularity at the metaphase of the first division of meiosis that the material was shelved as being unsatisfactory for use in teaching. When a similar irregularity was found in plants collected at Ames, Iowa, the latter material was examined with respect to certain details of this irregular meiosis.

MATERIALS AND METHODS

Anthers were killed in the following fluid:

1 per cent. chromic acid	50 cc.
Saturated aqu. picric acid	35 cc.
Formalin (C.P. 42 per cent.)	10 cc.
Acetic acid (C.P.)	5 cc.

In order to facilitate rapid penetration by reagents, the anthers were held submerged in the above fluid and sliced into the thinnest possible slices. Only the slices that remained submerged were used. The material was dehydrated, without washing, in grades of acetone (5, 10, 15 per cent., etc.), cleared in 5 grades of acetone-xylol, and embedded in paraffin. Rapid and progressive infiltration is obtained as follows: Pour melted paraffin (52° C.) over the cold xylol containing the tissues, forming a solid layer of paraffin about twice the volume of the xylol. At 35° C. saturation is attained in a few hours. Transfer to a 52° C. oven and complete the infiltration by decantation and replacement with melted 52° C. paraffin. The interval in the 52° C. oven should be less than four hours.

[1] C. D. Darlington, "Recent Advances in Cytology." Churchill, London, 1932.

[2] F. W. Sansome and J. Philp, "Recent Advances in Plant Genetics." Blakiston, Philadelphia, 1932.

Microtome sections of 5–8 μ were made and stained in gentian-violet-iodine. Certain stages were verified with iron-hematoxylin and with safranin-fast green. The preparations are undoubtedly inferior to the best smear technique, but comparison with published photomicrographs and measurements indicates that the phenomenon with which this paper is primarily concerned is shown with adequate accuracy.

OBSERVATIONS

The early prophases appear to be more or less "normal." The strands of the pre-meiotic reticulum bear diffuse chromatic granules of varying size. During the progressive transition from the reticulate condition to leptophase the outlines and linear arrangement of granules become clear-cut. Favorably located portions of the earliest leptotene strands exhibit a marked spiral twist (Figs. 1, 2, 3, 4). Synapsis begins at one end of a pair of homologues. During the subsequent progressive synapsing of the chromosomes, "homologous" granules, matched as to size and location, may be distinguished. Incomplete synapsis between a pair of chromosomes affords the best oppor-

EXPLANATION OF FIGURES

All figures are microsporocytes of *Lilium tigrinum*, ×560. The pen sketch interpretations are not drawn to scale.

FIGS. 1, 2, 3, 4. Transition from pre-meiotic reticulum to early leptophase. Spiral structure evident in selected strands.

FIG. 5 a, b. Mid-zygophase. Matched chromomeres on incompletely synapsed chromosomes.

FIG. 6 a, b, c. Mid-zygophase, photographed at two foci. Homologues are synapsed through about one half of their length. Note spiral twist of synapsed portion, and symmetry of the two free unpaired ends.

FIG. 7. Late anaphase of first division showing lagging "J" pair.

FIG. 8. Late anaphase of first division showing two lagging pairs, one pair clearly of the "I" type.

FIG. 9. Late anaphase. The lagging chromosome is in a peripheral position and has not yet become encircled by the developing partition wall.

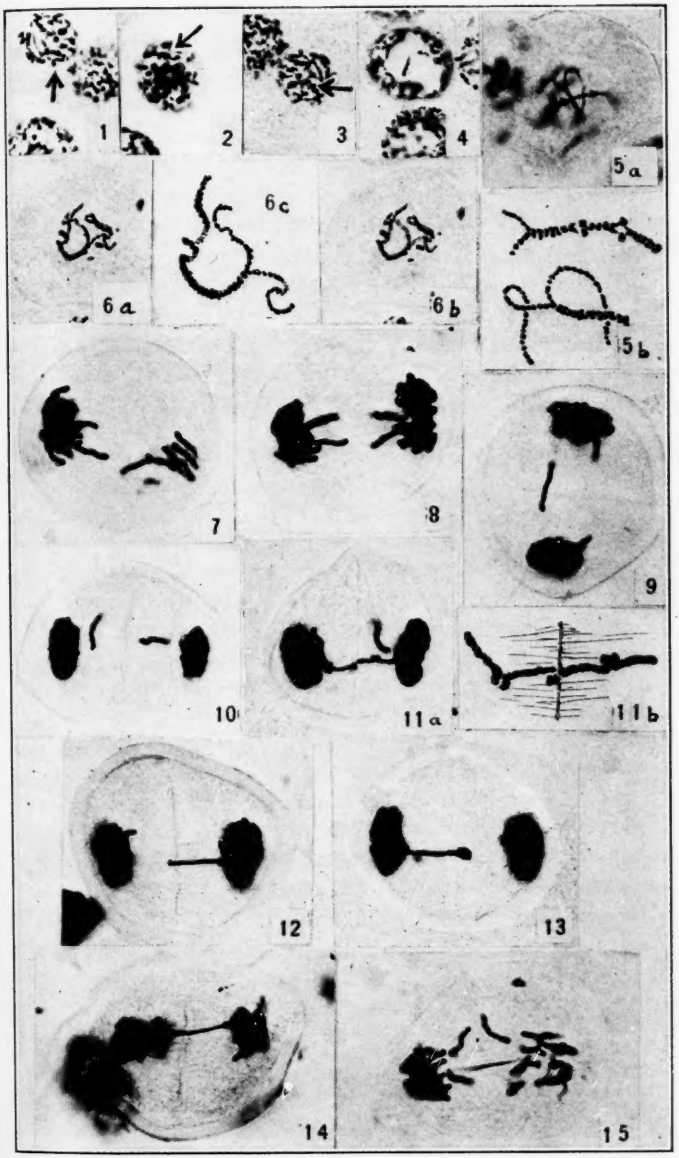
FIG. 10. Late anaphase, the lagging chromosomes are of the "I" type.

FIG. 11, a, b. Late anaphase. Two pairs of chromosomes had lagged. One pair is quite free of the partition wall. The members of the other pair were caught by the new wall and the four chromatids were opened out. The abstricted piece is not in focus in the photograph.

FIG. 12. Late anaphase. A highly attenuated chromosome held fast by the partition wall.

FIG. 13. Late anaphase. Constriction in chromosome produced by the girdling action of the wall. Note the bend in the new wall in the direction of pull.

FIGS. 14, 15. Attenuated chromosomes stretched from pole to pole.



FIGS. 1–15

tunity for observing the matched chromomeres (Fig. 5 a, b). The unsynapsed ends of a pair of chromosomes frequently exhibit symmetrical configuration, and the synapsed portion may exhibit a spiral twist. (Fig. 6 a, b, c).

In many pieces of anther all or most of the sporocytes were found to be in "synizesis." This contraction was observed in sporocytes in the early, polygonal, closely compacted stage, as well as in the older, elliptical, practically free-floating sporocytes. A careful comparison of the degree of shrinkage and of the quality of cytoplasmic and chromatin fixation in contracted and uncontracted nuclei indicates that synizesis is associated with shrinkage, coarse granulation and other evidences of poor fixation. A complete series of stages of prophase condensation of chromosomes can be built up without taking synizesis into account.

At the anaphase of the first division the most salient feature is the frequent occurrence of lagging of one or more pairs of chromosomes.[3] The lagging pair may be of the "J" type (Fig. 7) or the "I" type (Figs. 9, 10). Not infrequently one of the lagging chromosomes remains stretched across the median region of the sporocyte until after the partition wall has begun to form (Fig. 12). A constriction appears on the lagging chromosome, cutting off a piece of the chromosome (Fig. 13). In this case a piece of each of the two chromatids which make up the chromosome is cut off. There are cases in which one end of a chromosome is held by the developing partition wall, and the tension of the spindle fibers suffices to open out the two chromatids of the chromosome (Fig. 11). The abstricted fragment thus represents a piece of a chromatid. Occasionally, a single highly attenuated thread with an obscure spiral twist may be seen stretched from pole to pole. (Figs. 14, 15).

In most of the sporocytes there is no longer any indication of lagging at early telophase. Chromosome fragments are evident in some cells at the diad stage and in early microspores. Chromosomes remain "caught" in the much-thickened partition wall of the microspore tetrad, probably by the type of girdling illustrated in Fig. 13.

In view of the fact that these observations were made on microtome sections, in which chromosomes are inevitably cut,

[3] Dr. L. W. Sharp, of Cornell University, has kindly loaned the writer several slides of an unnamed species of lily in which similar irregularity occurs.

the writer is reluctant to figure the cells containing fragments or to estimate the incidence of fragmentation. It will be necessary to verify the later stages of meiosis by means of the smear method.

Discussion and Summary

Pollen mother cells of *Lilium tigrinum* exhibit an apparently normal leptophase and zygophase. The marked tendency of leptotene strands and synapsed bivalent threads to assume spiral twists indicates the presence of innate tensions, which may be the result of definite orientation of ultimate structural units. The frequent occurrence of mirror-image symmetry between unpaired portions of zygotene homologues suggests a coordinated emergence of homologues from the reticulate condition and implies a definite orientation of chromosomes in the reticulum.

Lagging of one or more pairs of chromosomes occurs at the anaphase of both divisions of meiosis. This phenomenon appears to be a delay, rather than a failure of the spindle mechanism, for there is a tardy poleward movement of the lagging chromosomes. This movement is accompanied by polar stresses that are sufficient to disjoin sister chromatids, to produce marked attenuation of chromosomes, and to displace a portion of the partition wall which may have encircled a lagging chromosome.

Observed cases of chromosome fragmentation were invariably the result of the girdling of lagging chromosomes by the partition wall. Girdling is probably accomplished by the closing of interfibrillar spaces during the formation of the new wall.[4]

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THE HORMONIC INHIBITION OF A SOMATIC CHARACTER IN THE CYPRINODONT FISH, *RIVULUS UROPHTALMUS*

During the last decade numerous investigations in the inheritance of color patterns and sex-linked characters in fish have been carried on. Our knowledge of genetic mechanism has advanced more rapidly than our understanding of the concomitant physiological processes. To-day very little is known of the physiological basis for sex differentiation in fish. It is

[4] After this paper was submitted for publication, the following paper, dealing in more detail with the later stages of meiosis, became available: Y. Takenaka, "On the Irregular Meiotic Division in the Pollen-mother-cells of *Lilium tigrinum* Ker-Garol." *Bot. Mag. Tokyo*, 47: 125–131. 1933.

the purpose of this note to give a preliminary statement of a study now being made of certain genetic and physiological factors underlying such sex-limited ocelli and mottlings as are found in many of the Cyprinodontidae.

The female *Rivulus urophtalmus* (Guenther) displays a perennial velvety-black ocellus in the dorsal region of the caudal fin base. The ocellus is entirely lacking in the normal male. In seeking to identify the determining factor for this distinct sex-limited character, several explanations may be considered: (1) that the female is genetically heterogametic for sex, and that the dominant gene for the character in question is located in the W (Y) chromosome, and is thus passed from mother to daughter; (2) that the differentiation is brought about by the specific action of a gonadal secretion, in this case, an ovarian hormone; (3) that the ocellus is an evolved somatic character potentially present in both sexes, but inhibited in the male by a testicular chalone.

To account for the apparent father-to-son inheritance in *Lebestes reticulatus,* Schmidt (1920) considered the male heterogametic for sex and presumed that the dominant factor for the male sex-linked character is located in the Y chromosome. Similar observations were made by Aida (1921) on *Aplocheilus latipes* and by Winge (1922, 1923) on *Lebestes,* the latter noting crossing-over between the X and Y chromosomes. Bellamy (1922, 1928) concluded from his observations that the mode of sex determination in *Platypoecilus maculatus* is of the WZ avian type. Fraser and Gordon (1928) and Gordon (1931) demonstrated the location of a factor in the W (Y) chromosome of a heterogametic female *P. maculatus,* which was presumed to have crossed over from the Z chromosome, thus accounting for the mother-to-daughter inheritance.

These extensive and apparently conclusive observations would lead one to assume by inference that a dominant gene determines the appearance of the caudal ocellus in the female *Rivulus urophtalmus* and that it should be located in the W (Y) chromosome of a WZ mechanism. In the light of certain facts, however, the writer is compelled to assume that the ocellus in *Rivulus* is sex-limited as a result of the physiological activity of the gonadal endocrine secretions. In *Amia calva* an activity very similar in form and position to that in *Rivulus* is found limited to the male. This would at first appear parallel to the Mendelian case described by Schmidt, *et al.,* in the male *Lebestes.* Zahl and Davis (1932) were, however, able to demonstrate by

gonadectomy that the ocellus in *Amia* is potentially present in both sexes, and that its appearance in the female is inhibited by an ovarian endocrine principle. It is further noted by Zahl and Davis that the ocellus is present in all sexually immature *Amia*, and becomes strictly sex-limited only with the advent of sexual maturity.

The writer considers the case of *Rivulus* parallel to that of *Amia*, rather than a case of Mendelian sex-linked heredity. There are two reasons for this view. First, an ocellus is present in juvenile *R. urophtalmus* of both sexes. In the male it fades to extinction with the coming of sexual maturity, and in the female it becomes somewhat elaborated. It is to be noted that this change is concomitant with the appearance of puberty, or the period of presumed high endocrine and germinal activity of the gonads. Second, in *Rivulus ocellatus* (a species very similar to *R. urophtalmus*) an ocellus is present in mature individuals of both sexes, but is less distinct in the male than in the female. The inhibitory action of the testicular secretion appears, in this case, to be incomplete and poorly developed. These observations appear to indicate that the caudal ocellus in *R. urophtalmus* is an evolved somatic character potentially present in both sexes, but inhibited in the male by a secretion elaborated by the mature testis.

The experimental procedure being followed in investigating the specific relation between the gonads and the caudal ocellus in *Rivulus* is one employing such devices as gonadectomy, injection of gonadal extracts, transplantation and breeding. The results of these experiments will be published *in extenso* on a later date.

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HAIRLESS MICE AND ULTRA-VIOLET LIGHT

IN 1929 I decided to experiment with hairless mice to see if through successive generations they would acquire resistance to ultra-violet light. For this purpose a strain of hairless mice was obtained from the Bussey Institution of Harvard University. The strain was divided into two groups. One group was subjected to ultra-violet light for six generations; the other group was not. Three animals from two litters of the sixth irradiated generation and two controls of the same age were irradiated together in the same cage. On successive days they were given the following doses of irradiation (using as source a quartz mercury burner); 5, 15, 20 and 25 minutes at a distance of 29 inches on the first four days; 25 minutes at 26 inches on the fifth day; 25 minutes at 20 inches on the sixth day; 30, 40, 72, 50, 77, 78 and 93 minutes on the seventh and thirteenth days; 25 minutes and 30 minutes at 20 inches with a new quartz mercury burner on the fourteenth and fifteenth days. Slight peeling began on the controls after one exposure, but in the experimental animals not until after 4 exposures. The controls also tanned more rapidly. The reduction in duration of the tenth exposure was necessitated by the very severe burning and peeling of the controls. One control developed a sore from the burns after ten exposures. At the end of the 15 exposures, while the controls were severely burned, the experimental animals were only slightly so. Moreover, the burns disappeared within six days and left the animals quite normal. On the other hand, the controls developed hard raised callouses diagnosed by Dr. D. M. Gay as hyperplasia of the epithelium.

The great difference in response to irradiation between the irradiated and control mice may have been due to the inheritance of acquired resistance to irradiation. On the other hand, it may have been due to inadvertent selection of animals genetically diverse with respect to resistance to irradiation. Or, finally, the difference may have been purely a random difference such as might be found among any large sample of the same stock. It should be noted that each successive generation of mice subjected to irradiation withstood larger and larger doses as re-

corded below. The results are clearly inconclusive and do not permit of a decision as to these three alternatives. However, in view of the importance of the issue, they may be sufficiently suggestive to stimulate others to repeat and extend the work.

For those interested in such an experiment, it will be helpful to know that after many trials of diverse techniques the following method of irradiation was found most successful: Use a quartz mercury burner.[1] Expose the mice in open wire cages with strips of tin at the top to prevent their escape so that the center of the quartz burner is 12 inches from the bottom of the cage. The light is passed through quartz plates over which a thin stream of water is passing to remove the infra-red rays. If the water filter is not used the distance should be increased to 29–30 inches. Each litter was exposed to the light from the moment that the young had shed their hair. I started with a dose of two minutes' duration, increasing the dose by one minute each day until eurethemia and slight peeling developed. Irradiation was then omitted for one or two days and then resumed. As the duration of the dose became larger, it was sometimes necessary not only to omit treatment for a day or two but to reduce the time of exposure. It was found desirable to keep the temperature of the laboratory where the mice were kept at about 80°, also to provide abundant food with regular quantities of lettuce and cod liver oil. The experiments were conducted over a two-year period. Careful records of the exposure of each subject to the ultra-violet light were kept and at the conclusion of the experiments it was discovered that the average exposure per day[2] increased in each successive generation from an average of 13 minutes in the second generation, 18 minutes in the third generation, 21 minutes in the fourth generation, 25 minutes in the fifth generation, and about 30 minutes in the sixth generation.

For the benefit of any who may be interested in hairless mice, a brief bibliography on the subject is given herewith.

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[1] I used a Luxor Alpine Lamp manufactured by the Hanovia Company (S. C. 2300).

[2] The amount of ultra-violet light given each day added together during the total life of the mice and divided by the total number of treatments.

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CORRECTION.

On page 56 of volume LXVIII (January–February, 1934) the equation near the center of the page should read

$$x = 1 + \frac{2}{\sqrt{\pi}} \int_0^t e^{-t^2}\, dt.$$